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Proceedings of the Second US-USSR
Symposium on:

Air Pollution Effects on Vegetation

Including
Forest Ecosystems



edited by

Reginald D. Noble

Juri L. Martin

Keith F. Jensen

*Proceedings of an International Conference
Corvallis, Oregon; Raleigh, North Carolina; Gatlinburg, Tennessee
September 13 - 25 , 1988*

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AIR POLLUTION EFFECTS ON VEGETATION

Including Forest Ecosystems

Proceedings of the Second US-USSR Symposium

Edited by

REGINALD D. NOBLE

US Project Leader

Bowling Green State University, Bowling Green, Ohio

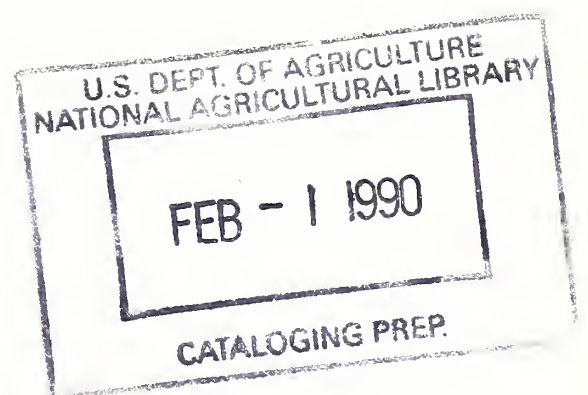
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Soviet Project Leader

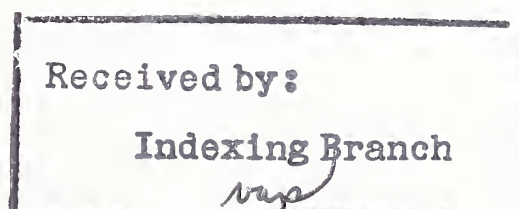
Tallinn Botanical Garden, Estonian SSR Academy of Sciences, Tallinn, Estonia

KEITH F. JENSEN

US Department of Agriculture, Forest Service, Delaware, Ohio



September 1989



Preface

At the Tenth Meeting of the US-USSR Joint Committee on Cooperation in the Field of Environmental Protection, held in Washington, D.C. in 1986, Dr. Juri Martin and I agreed that our project (Project 02.03-21) should organize a symposium in the United States to commemorate the tenth year of cooperation on this project. The major objectives of the symposium were to acquaint scientists on the two sides with project accomplishments, to promote understanding of the nature of environmental problems that relate to air pollution effects on vegetation on a more global scale, to share research priorities, interests, and methodologies and to plan future research cooperation.

It was decided that holding a "traveling" symposium at three different locations would make it possible to expose a greater number of the U.S. scientists to the Soviet delegation as well as increase the exposure of the Soviet scientists to a broad spectrum of research endeavors and research facilities in the U.S. The Corvallis site offered a U.S. Environmental Protection Agency research facility, and a U.S. Department of Agriculture, Forest Service Research Station; the Raleigh site offered a U.S. Department of Agriculture Research Service Facility; and the Gatlinburg site offered an intensively studied national park and a national laboratory. Furthermore, all were near major universities where relevant research is also being conducted.

Planning for the symposium began in earnest in 1987 with the formation of a Symposium Planning Committee. Upon the advice of the committee, the symposium sites were selected, the themes were identified, programs were planned, speakers were selected, and funding sources were sought. By spring, 1988, funding was committed and by early summer, major arrangements were complete.

I wish to express my gratitude to the Symposium Planning Committee for the expert job they did. The committee members were: Ann Bartuska, Roger Blair, Keith Jensen, and David Shriner. I am pleased to have had the opportunity to have chaired this committee, and count it an honor to have worked with such dedicated and capable individuals.

Reg Noble

Acknowledgements

The success of this symposium can be attributed, in large part, to the local organizers: Roger Blair, Ann Bartuska, Dave Shriner, and their associates. Their thoughtful contribution to development of the program, their expert assistance in selection of speakers, and their careful handling of local arrangements were vital to the success of this conference. Technical assistance with preparation of the manuscripts for publication was provided by Lorraine DeVenney, Tom Howe, Dan Lange, Diana Peh, and Jane Trumbull. Editorial assistance was provided by Leon Dochinger, Roy Patton, Beverly Stearns, and Mary Buchanan.

Financial support for the symposium, which included hosting the Soviet participants, was provided by the U.S. Environmental Protection Agency, the U.S. Department of Agriculture Forest Service (Northeastern, Southeastern and Pacific Northwestern stations), the Environmental Sciences Division of the Oak Ridge National Laboratories, Bowling Green State University, Oregon State University, the National Council of the Paper Industry for Air and Stream Improvement, the Edward Lamb Foundation, Dr. Anthony Joseph, the Electric Power Research Institute, the National Park Service, and BP America. Publication of the proceedings was made possible by funding provided by the Forest Response Program, Bowling Green State University and the U.S. Environmental Protection Agency.

The editors extend sincere thanks to each (named and unnamed) for their support. Without their help, the symposium and publication of its proceedings could not have occurred. Also, thanks are extended to our Soviet colleagues for their participation with special thanks to Soviet Project Leader Martin for coordinating arrangements for the Soviet side.



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Introduction

Juri Martin

USSR Project Leader

Reginald Noble

U.S. Project Leader

The Agreement between the USA and the USSR on Cooperation in the Field of Environmental Protection was signed in Moscow on May 23, 1972. This treaty-level agreement states that "the sides will develop cooperation in the field of environmental protection on the basis of equality, reciprocity and mutual benefit" and that "this cooperation will be directed towards solving the most important aspects of environmental problems and will be dedicated to the development of measures for preventing environmental pollution, to the study of pollution and its effect on the environment, and to the development of the bases for controlling the impact of man's activity on nature."

The results of this cooperative effort since its inception were reviewed at the Tenth Joint Committee meeting which was held in Washington, D.C., USA, December 1986, and again in Moscow, USSR, February 1988. A constructive review of environmental problems of international significance was held during both meetings. The two sides confirmed the declaration made by the Joint Committee in September 1972 in which it is stated: "The people and the governments of both countries consider it of utmost importance to ensure the responsible use of natural resources and the protection of

nature under conditions of technical and economic progress. The sides will cooperate with each other and with other interested countries with the objective of the joint use of research results and in advancing the environmental protection effort in general."

The Joint Committee acknowledged the special importance of cooperation on selected global problems such as stratospheric ozone depletion and other possible climate change associated with anthropogenic impacts, pollution of the world oceans, and the problem of acid rain and forest decline. Consistent with this declaration, efforts were initiated in 1977 to establish a project on "Interactions Between Forest Ecosystems and Pollutants." In 1978, this project was formally established (Project 02.03-21) and the first cooperative exchanges took place. A US delegation composed of Dr. Leon Dochinger, the US Project Leader, USDA Forest Service, Dr. Leonard Weinstein, Boyce Thompson Institute of Plant Research and Dr. Walter Heck, North Carolina State University, visited the USSR. Later that year, a Soviet delegation composed of Project Leader Dr. Vladislav Alexeyev, Komarov Botanical Institute of the Academy of Sciences, USSR, Dr. Juri Martin, Tallinn Botanical Garden of the Acad-

emy of Sciences of Estonian SSR, Dr. Alexander Salov, Academy of Sciences of USSR and Nicolai Prilepo, Ministry of Forestry of the Russian FSSR visited the United States for two weeks. The major goals of this exchange were the following: to acquaint the two sides with current research activities and to identify those areas of research that have greatest potential for future cooperation; to observe field research sites and laboratories; to plan cooperative research activities and identify areas of cooperation to be focused upon for the next year and following five year period.

The objectives of the project were discussed in these early meetings and have evolved into a set of cooperative endeavors between the two countries, which are contributing to the furthering of our understanding of the impact of air pollution on the biosphere. They include:

- the impact of air pollution on vegetation
- the mechanism of action of pollutants on vegetation
- the role of vegetation in amelioration of air pollution
- the management of ecosystems damaged by air pollution
- the response of plants to air pollutants in conjunction with other environmental variables such as light, moisture, nutrition, CO₂ and temperature

In 1979, there were two exchanges. A two-member American delegation composed of Drs. Dochinger and Reginald Noble, Bowling Green State University, visited the USSR for two weeks. They visited research laboratories and air pollution impact sites in Moscow, Leningrad, Donetsk and Kishinev. Later in 1979, Soviet Project Leader, Dr. Alexeyev along with Dr. Yevgeny Miroslavov of the Komarov Botanical Institute of the Academy of Sciences, USSR in Leningrad, were hosted by Dr. Noble at Bowling Green State University where they engaged in physiological research for six weeks. They also had an opportunity to visit other

university research laboratories for the purpose of identifying other possible joint projects. Among the working groups to be established, it was conceived that anatomical, and particularly ultrastructural, studies would comprise one important research thrust in understanding the environmental impact of air pollutants on vegetation – especially forest species and agricultural crop plants. During, and subsequent to these two exchanges, Drs. Richard Crang and Jong Yoon of Bowling Green State University (Ohio) were invited to take specimens of sulfur dioxide-fumigated hybrid poplar (*Populus deltoides* x *P. trichocarpa*) leaves to the Komarov Botanical Institute laboratories in Leningrad for ultrastructural study. That work, which was conducted in 1980, set the stage for productive collaborative investigations that have continued to the present. The original Soviet participants from the Komarov Botanical Institute were Drs. Maria Danilova, Miroslavov and Andrey Vassilyev. Later Dr. Irina Kravkina, also from the Komarov Botanical Institute, became active in the project.

In May, 1981, US Project Leader Dr. Dochinger and Dr. Noble visited the USSR. They were acquainted with laboratories and field research sites in Leningrad, Tallinn (Estonian SSR) and Dushanbe (Tadjik SSR). During this visit, the American delegation worked with Drs. Alexeyev and Martin on a book manuscript planned for publication in 1982. They also worked on plans for the First US/ USSR Symposium on project 02.03-21, scheduled for autumn 1982. Following the visit of the American delegation, a Soviet delegation visited the USA between October and November of 1981. The delegation was headed by project leader Dr. Alexeyev and consisted of Drs. Danilova and Kravkina. During this visit, Dr. Alexeyev conducted physiological research in the laboratories of Drs. Noble (Bowling Green State University, Ohio) and Dochinger (USDA Forest Service Research Laboratories, Delaware, Ohio). Drs. Danilova and Kravkina continued ultrastructural investigations in the

laboratories of Drs. Crang (University of Illinois) and Noble (Bowling Green State University, Ohio). SO₂-fumigated plant materials were prepared for transfer to the USSR for further investigations. The results of this work have since been published.

In October of 1982, a ten-member American delegation visited the USSR to participate in the First USSR/US Symposium on "Interactions Between Forest Ecosystems and Air Pollutants." The delegation consisted of Drs. Dochinger (US Project Leader), Noble, Crang, Jay Jacobson, Donald Davis, David Karnosky, David Shriner, William Smith, Daniel Houston, and James McClenehan.

The Symposium was held in the cities of Leningrad, Tallinn and Puschino-on-Oka. The Symposium permitted scientists from the two sides to discuss current air pollution problems and to exchange results of recent independent and cooperative research. There were 24 formal paper presentations, ten by Americans and 14 by Soviets. Five additional reports were given by the American scientists upon the request of the Soviet side. Three volumes containing research reports and abstracts were published by the organizers and distributed during the symposium. Reports presented at symposium were received with great interest and generated provocative and intense discussion.

The USSR was represented by Drs. Alexeyev (USSR Project Leader), Martin, George Ilkua, Victor Tarabain, Valeri Uchvatov, Ljudmila Martin, Eva Nilson, Nikita Glarovsky, and Oleg Chertov.

After the discussion at the symposium, the main areas of collaborative research were identified. They included plant physiology, anatomy, forest ecology, soil sciences and lichenology. During the symposium, a desire to continue the exchange of delegations during 1983-1984, and beyond, was jointly expressed. Also,

it was agreed that a second symposium should be held in the United States in 1985. None of these objectives was accomplished.

In 1985, two American scientists, Drs. Noble and Crang visited the USSR. Dr. Crang worked at the Komarov Botanical Institute in Leningrad to continue research and review previously collected anatomical data and electron micrographs and to organize materials for a joint article with Drs. Danilova, Vassilyev, and Kravkina.

Dr. Noble also visited Komarov Botanical Institute to finalize and edit two papers on light and SO₂ effects on photosynthesis based upon work performed jointly with Dr. Alexeyev in Dr. Noble's laboratory in 1981. In addition, Dr. Noble worked at the Tallinn Botanical Garden, Estonian SSR Academy of Sciences, Tallinn, with Dr. Martin. While in Tallinn, Dr. Noble visited Tartu State University and the laboratory of biophysics at the Institute of Astrophysics and Atmospheric Physics, Estonian SSR Academy of Sciences. Dr. Agu Laisk, head of this laboratory, demonstrated unique instrumentation for photosynthesis research. During the discussions, the two sides reaffirmed the importance of continuing and expanding their efforts in the areas mentioned above.

The 1985 year closed with the Ninth Session of the Joint Committee Meeting in Moscow where the program for cooperation in 1986 was prepared. At this Joint Committee Meeting, Drs. Noble and Martin assumed their new roles as project leaders (Noble had been appointed to this position in November 1982).

In September 1986, an American delegation consisting of Drs. Noble, Crang and Thomas Nash visited the USSR for a period of two weeks. The objective of Dr. Crang's visit was to continue the anatomical research in Komarov Botanical Institute with the plant anatomy group headed by Dr. Danilova. Dr. Crang spent most of his time conducting research and preparing

manuscripts in cooperation with Drs. Danilova, Vasilyev, Kravkina and Miroslavov. Dr. Nash had an opportunity to study at the lichenological herbarium at Komarov Botanical Institute in Leningrad and then, with Drs. Noble and Martin, to visit field sites in Tallinn and Tartu in Estonia and Sochy (Caucasus area). In Sochy, the American delegation was accompanied by Drs. Oleg Blum (Holodny Botanical Institute, Ukrainian SSR Academy of Sciences, Kiev) and Stepan Shiyatov (Institute for Plant and Animal Ecology, USSR Academy of Sciences, Ural's Division) to discuss possibilities of future continued cooperation in the field of lichenology and to institute new cooperation in dendrochronology.

Project leaders from both sides took part in the Tenth Joint Committee Meeting in Washington, D.C. in December, 1986. At this meeting, the new title of Project 02.03-21 was changed to: "Air Pollution Effects on Vegetation—Including Forest Ecosystems." In addition, Dr. Martin visited the Arizona State University, Tempe, Arizona, where he had productive discussions with Dr. Nash on continuing joint efforts in lichenology. He also visited the University of Arizona (Tucson, Laboratory of Tree-Ring Research) for planning cooperative research in dendrochronology with Dr. Malcomb Hughes, Director of the Laboratory of Tree-Ring Research, Harold Fritts, and Donald Graybill.

In 1987, the first exchange occurred in April when Drs. Miroslavov and Kravkina from the Komarov Botanical Institute were hosted by Dr. Crang at the University of Illinois. Their visit was for the purpose of fumigation and preparation of specimens for ultrastructural investigations. It was agreed that the current efforts on sulfur dioxide effects on foliar structures should be concluded as soon as appropriate specimens were examined. It was also anticipated that the work would be presented as part of the second US/USSR Symposium held in 1988 in the United States.

In accordance with joint activities planned

in 1987, a Soviet delegation composed of Drs. Martin, Laisk, Molley Mandre (Head of Ecophysiology Laboratory, Tallinn Botanical Garden, Estonian SSR Academy of Sciences) and Rodion Karaban (Head of Forest Ecology Research Group, Institute of Applied Geophysics, USSR State Committee of Hydrometeorology, Moscow), visited the United States. The major goals of this exchange were to acquaint the two sides with current research activities, and to observe and participate in field and laboratory research that might lead to major cooperative research efforts.

The delegation visited the US EPA Environmental Protection Laboratory, USDA Forest Service and the Oregon State University, Corvallis, Oregon. Drs. Laisk and Mandre engaged in research at Corvallis in cooperation with Drs. Roger Blair and William Hogsett on the influence of SO_2 on photosynthetic gas exchange and the effects of SO_2 on carbohydrate metabolism. They continued this work after two weeks at the USDA Forest Service Laboratories in Delaware, Ohio with Dr. Keith Jensen and Dr. Ken Loats.

During this time, Drs. Martin and Karaban were visiting field sites and research laboratories at the Great Smoky Mountains National Park, and the Ohio State University at Wooster. In Wooster, they visited field research sites in a high pollution impact region along the Ohio River, and in the Great Smoky Mountains National Park, they visited some of the most advanced air monitoring facilities currently in operation, and visited sites where red spruce is in a state of decline. The full delegation then came together and proceeded to the Boyce Thompson Institute in Ithaca, New York. The delegation then traveled to Whiteface Mountain and to Burlington, Vermont, to visit field sites, including Camel's Hump where evidence of red spruce decline was observed. At each of these locations, seminars were presented by scientists from both sides and free interchange of ideas and information occurred.

In September, a Soviet delegation consisting of Drs. Blum from Holodny Institute of Botany of the Ukrainian SSR Academy of Sciences and Shiyatov from the Institute for Plant and Animal Ecology of the Ural's Division of the Academy of Sciences of the USSR arrived in the US for a 90-day stay. Dr. Blum's work at Arizona State University and the Oak Ridge National Laboratory went very well. While at the Arizona State University, Dr. Blum learned the CO₂ depletion technique for quantifying photosynthesis and respiration in lichens. During his visit at ORNL, laboratory work was completed for a project that compared the trace metal contents of lichen species collected in the Great Smoky Mountains National Park in 1939, 1966 and 1982. This work was done with the support and collaboration of Drs. Shriner and Lorene Sigal.

Dr. Shiyatov's work at the University of Arizona's Laboratory of Tree-Ring Research is one of the highlights of cooperation to this date. The principal objectives of this exchange were to compare various standardized methods, in particular the Corridor Method, developed and used by Dr. Shiyatov to obtain the Ural chronologies, with the methods developed and used at the Laboratory of Tree-Ring Research, and to cooperate in analyzing and evaluating the effects of pollutants on the radial growth of trees at various distances from point pollution sources. This exchange resulted in the exchange of data, statistical models and ideas that proved extremely valuable to both parties.

In accordance with activities planned in 1988, an American delegation comprised of Drs. Noble and Jensen visited the USSR for two weeks in June. This delegation visited Tallinn Botanical Garden and the laboratory of Dr. Laisk in Tartu. In Estonia, final plans were made for the second symposium. Next, the US delegation traveled to Irkutsk where Drs. Noble and Jensen were acquainted with the research work in the Siberian Institute of Plant Physiology and Biochemistry. Of particular interest was the

current research on the impact of fluoride emissions on forest trees. Drs. Noble and Jensen gave seminars at this institute, and problems connected with air pollution impact research were discussed. The American delegation had a one-day tour of the region, including a boat excursion on Baikal Lake. Finally, the American delegation visited Kiev. This visit was hosted by Dr. Blum from the Central Botanical Garden of the Ukrainian Academy of Sciences.

Two other American visits to the USSR occurred in 1988 under Project 02.03-21. Joint field work in the Kirgisian mountains for the collecting of dendrochronological core samples by Drs. Graybill from the University of Arizona's Laboratory of Tree-Ring Research and Shiyatov from the Institute of Plant and Animal Ecology of the Ural's Department of the USSR Academy of Sciences, Sverdlovski, took place for one month. This exchange was very successful and will result in publication. At approximately the same time, Dr. Crang was in Leningrad at the Komarov Botanical Institute where he presented leaf samples fumigated in his laboratory. These samples were subjected to analysis by electron microscopy. The two sides also worked on manuscripts which were being prepared for publication. In Leningrad, Dr. Crang discussed the possibility for collaborative work with U. Kallavus from Tallinn Technical University.

Over the past ten years, cooperative efforts by the two sides have been productive; and possibly more importantly, they have laid the groundwork for very important future cooperation. It is expected that work will intensify in those research areas already identified and that it will expand into new areas such as global climate change.

Session

I

Dendrochronology—Tree Rings and Environment

Roger Blair, Jeff Brandt, Beverly Law, Local Organizers

Introduction

The field of dendrochronology was chosen for the theme of the first portion of the USSR/USA Symposium. The choice was appropriate in that both countries have made substantial recent progress in developing the tools and techniques of dendrochronology to help unlock the influence of climate and other factors on tree growth. The meetings began with formal presentations covering the state of the science of dendrochronology as well as the appropriate use of statistical procedures in dendrochronological analysis. These presentations set the stage for lively discussions about the use of

dendrochronology in future analyses of stresses on forested ecosystems.

The scientific interchange begun several years ago in this field continues today. New data sets and new analytical procedures will continue to improve the international effort in understanding the potential impacts of the greenhouse effect (global climate change) and air pollution in the world's forest resources. The symposium provided both an opportunity to summarize existing research as well as plan future cooperation.

Roger Blair

U.S. Forests and Atmospheric Deposition

Jack K. Winjum

EPA Environmental Research Laboratory,
Corvallis, Oregon, U.S.A.

Forests in the United States occupy 33 percent of the nation's land area and exist on some lands in all fifty states (USDA Forest Service, 1982). In total, they cover approximately 299 million hectares and are rich in essential resources such as water, wildlife, timber and recreation opportunities.

In general, U.S. forests may be divided into three large regions (Figure 1):

1. The Eastern forests consisting of the northern mixed conifer-hardwood type, the central mixed hardwood type and the southeastern pine type. The total area is 156 million hectares.
2. The Western forests which are predominately coniferous types divided between the Rocky Mountains and the areas along the Pacific Coast. These forests occupy 94 million hectares.
3. The Alaska forests which are a combination of coastal conifer types and interior mixed with conifer-hardwood types for a total of 49 million hectares.

The Eastern and Western forests lie between the 30th and 49th latitudinal parallels and, therefore, are predominantly in the temperate vegetation zone (Good, 1964). How-

ever, small areas of tropical forests exist in southern Florida and in Hawaii, and the interior forests of Alaska are boreal.

Historically, climates and mountain ranges have had a major influence on forming forests. In the U.S., the West Coast climate is maritime with cool winters of heavy precipitation and short dry summers. Eastward across the 48 contiguous states, the climate is continental with quite cold winters and hot, humid summers. Major mountain complexes are the Appalachian Mountains which parallel the East Coast, the stairstep order (low-to-high) of the Pacific Coast Range, the Cascade Range-Sierra Nevada and the Rockies in the West, and the Aleutian-Alaska Ranges along the Pacific coast of Alaska with the Brooks Range in the northern interior.

In total, the U.S. forests represent about 10 percent of the world's 2.85 billion hectares of forests. By comparison, the USSR has 790 million hectares of forest lands or nearly 28 percent of the world's total (USDA Forest Service, 1973).

Superimposed over the natural distributions of U.S. forests is the human infrastructure. Ownerships include federal, state, municipal and private lands. In broad terms, the federal

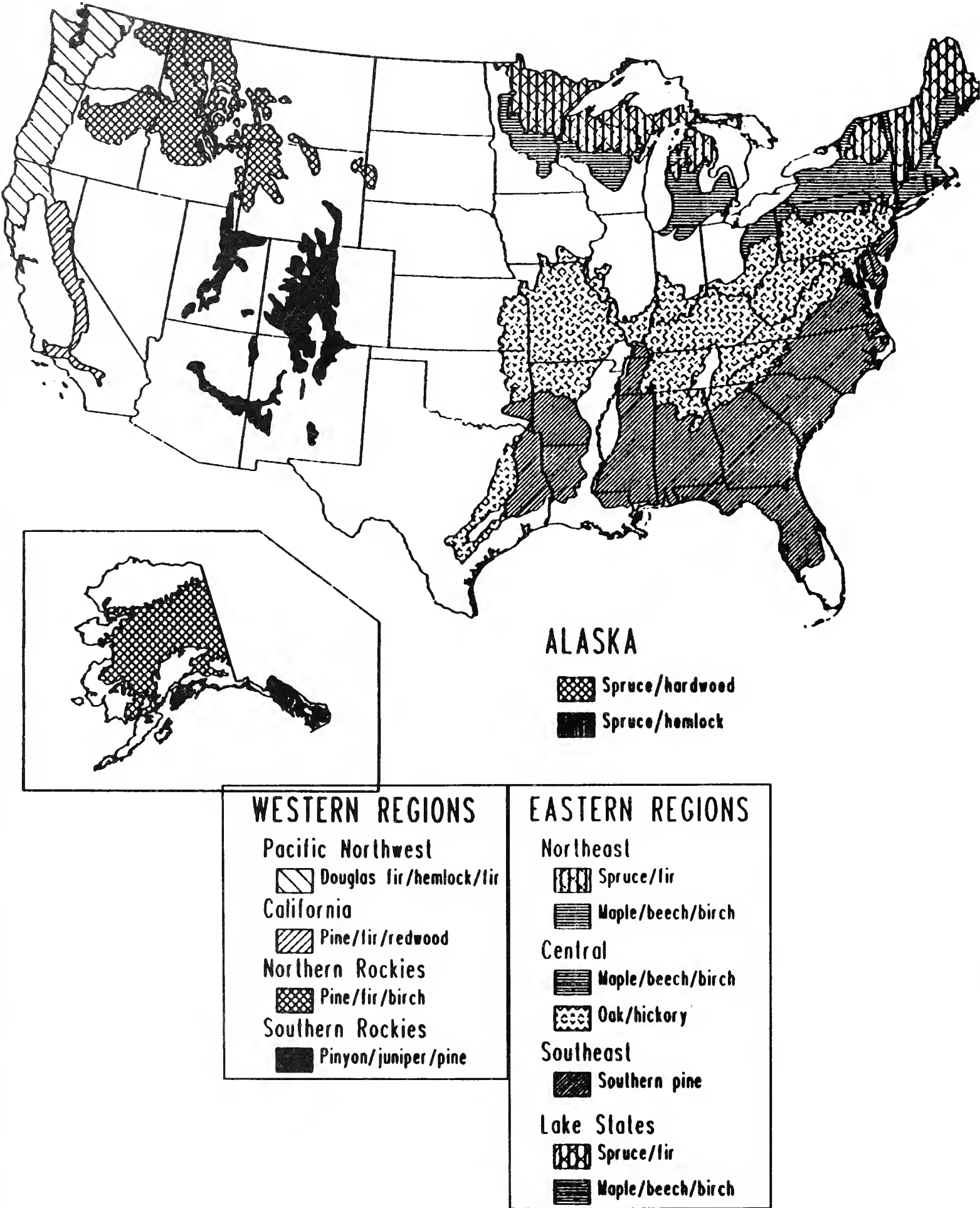


Figure 1. Major Forest Regions of the United States and Their Primary Tree Groups

government owns 21 percent of nation's forest lands, state and municipal represent 8 percent, large private ownership (i.e. the forest industry), 14 percent, and small private ownership, the largest at 57 percent. Much of the latter consists of parcels less than 200 hectares in size. Such a complex system of multiple ownerships is rare among the forested nations of the world and, while fundamental to a free society, often presents a significant obstacle to developing and implementing nation-wide forest policies.

Overall, U.S. forests are highly productive, providing a high degree of ecological diversity as well as abundant wood, water and recreation to meet basic human needs. Forest health, with few exceptions, has generally been good through the first two-thirds of this century. Indeed, forest science has developed the technology to double or triple the wood yields in many areas of commercial forest land over that of natural stands while maintaining or increasing the productivity of other forest resources.

However, in recent decades, several cases of forest decline on a regional scale have occurred in the U.S. which are not easily explained by normal natural causes. Examples are the pine-fir forests of the southern Sierra Nevadas in California and red spruce-true fir forests of the Appalachian Mountains in the East (NAPAP, 1987). In these cases, significant foliar damage has occurred and in some instances this has led to growth losses and increased mortality throughout many stands. To a lesser degree, the same symptoms have been noted in several other forest regions.

Atmospheric deposition of air pollutants is suspected to play a causal role in many of these cases. The evidence, however, is largely circumstantial in that forest areas with decline symptoms are frequently located where the deposition of pollutants is high. It must be remembered, though, that in many of these areas, stresses due to natural factors such as drought or winter cold extremes also occur.

Pollutants of concern are compounds resulting from anthropogenic emissions of sulfur dioxide (SO_2), oxides of nitrogen (NO_x) and volatile organic compounds (VOCs) including associated oxidants such as ozone (O_3). Both wet and dry depositions may be involved. Furthermore, combinations of these pollutants with natural factors, as mentioned above, are likely possibilities.

Proof of cause and effect has been illusive. Ozone at concentrations elevated by human activities has been proven to cause declines in the ponderosa-jeffrey pine stands in the southern Sierra Nevadas in California and in the eastern white pine throughout the eastern U.S. But many other wide-spread declines remain unresolved.

Forestry research programs have addressed the issue over the last 25 years and most intensively during this decade. A comprehensive summary document on the air pollution situation in the U.S. is under preparation by the National Precipitation Assessment Program (NAPAP). Plans call for publications in 1990. Sections on forest effects will form some of the fundamental portions of the 1990 Assessment Document. Based on this information, U.S. policy makers will make new decisions about the need for more intensive regulation of air pollutant emissions.

Literature Cited

- Good, R. 1964. *The geography of the flowering plants*. John Wiley & Sons, NY. 518 pp.
- USDA Forest Service. 1982. *An analysis of the timber situation in the U.S. 1952-2030*. Forest Resources Report No. 23. 499 pp.
- USDA Forest Service. 1973. *Outlook for timber in the United States*. Forest Resources Report No. 20. 350 pp.
- NAPAP (National Acid Precipitation Assessment Program). 1987. *Forest Effects. Interim Assessment*, Volume IV, Chapter 7. p. 1-7 to 7-59.

Comparative Analysis of the Standardization Methods of Tree-Ring Chronologies

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Many variations in tree-ring widths can be attributed to fluctuating climatic conditions, but forest stand conditions, increasing tree age and various disturbances also produce marked ring-width variations. These nonclimatic sources of variations usually produce slowly changing trends in growth through time. It is important in climatic reconstruction work that the nonclimatic trends be identified as much as possible, separated from the effects of climatic factors, and removed so that the remaining variations are faithful representations of the climatic factors.

The most popular method of ring-width standardization is to fit a curve, either graphically or mathematically, to the ring widths plotted as a function of time (Fritts, 1976). This method can be subjected to rigorous computer analysis and objective statistics can be used to describe the results. The ring widths are divided by the value of the fitted curve to obtain standardized growth indices. This method is used at the Laboratory of Tree-Ring Research, University of Arizona (programs INDEX and ARSTAN).

Program INDEX fits a negative exponential curve, a straight line or a polynomial curve to the data and then calculates the arithmetic mean of the indices to obtain the final chronology (Graybill, 1982). Program ARSTAN begins by fitting a similar exponential curve and straight line. It calculates the indices and can fit a second spline curve to the indices if there are any remaining low-frequency features. This second curve is generally a ridged spline removing 50% of the variance at periods of 2/3 the length of a ring-width record (Cook, 1985; Holmes *et al.*, 1986). In addition, ARSTAN applies ARMA modeling and uses a robust estimation of the mean to combine the indices of individual cores and trees into a single chronology.

Shiyatov (1972, 1986) proposed another method for calculating the growth indices. It uses the maximum and minimum possible range of the ring-width data, which are estimated from curves fit to these two extremes of the data. These curves form a strip or a "corridor," so it is referred to as the CORRIDOR method. The width of the corridor varies regularly with the tree age, reaching its maximum during the

period of greatest growth. The corridor displays a range of growth in response to environmental fluctuations at different times throughout the life span of the tree. The location of the actual growth for each year within the corridor is taken into account by subtracting the minimum curve from the ring width, multiplying by 2 (for a range of 0 to 200) and dividing the result by the difference between the curves for the maximum and minimum. Until now, plots of ring widths were estimated using human judgment, and the maximum and minimum possible curves were drawn by hand. The technique also has a mathematical solution.

If tree ring chronologies from the US and the USSR were to be compared or used jointly in project 02.03-21, "Air Pollution Effects on Vegetation," it was necessary to evaluate any differences in the methodology. While Shiyatov was visiting the Laboratory of Tree-Ring Research in 1987, we carefully examined and compared these three methods of standardization. The ring-width data came from Siberian larch (*Larix sibirica* Lbd.) growing at the upper timberline in various provinces of the Ural Mountains (Polar, Subpolar, North and South Urals), but all grew on relatively moist sites (with running water). The mean chronology indices (Table 1) basically reflect the thermal conditions of the summer months (Shiyatov, 1986).

The three methods were used to generate

three chronologies from each of the four sites (Table 2). The spline stiffness used in the second detrending of ARSTAN was 100% of the series length so maximum low frequency information was retained in these chronologies.

A visual comparison of the plots of indices, an analysis of the main chronology statistics, and a power and cross-power spectrum analysis (Blackman and Tukey, 1958) were used to evaluate the similarities and dissimilarities between the tree-ring chronologies.

The signal-to-noise ratio (the chronology variance/error variance) (Table 2) is approximately the same (from 22.9 to 29.2) for the three chronologies from the Polar, Subpolar and North Urals. The ratio was only 8.9 for the chronology from the South Urals. This difference in signal-to-noise ratio allowed us to evaluate the effects of standardization techniques on chronologies with varying amounts of climatic variation.

One can see from Table 2 that the chronologies developed by the CORRIDOR method have a little higher mean sensitivity and standard deviation as compared with the chronologies developed by the INDEX and ARSTAN programs. This difference is connected with the fact that the lower limits of the CORRIDOR method must pass through the minimum values, which are zero or positive values, while the lower limits for INDEX and ARSTAN are always

Table 1. Characteristics of the mean tree-ring chronologies

Series Code	Province	Latitude North	Longitude East	Altitude meters	Trees sampled	Chronology time span
S01	Polar Urals	66°50'	65°30'	150-300	21	1541-1968
S08	Subpolar Urals	64°40'	59°50'	550-700	20	1691-1969
S11	North Urals	59°35'	59°10'	800-950	25	1590-1969
S29	South Urals	54°30'	58°50'	1000-1100	11	1770-1972

Table 2. Statistics of the mean chronologies developed by the various standardization methods (C-CORRIDOR, I-INDEX, A-ARSTAN)

Series Code	Standardiza- tion Method	Mean Sensitivity	Standard Deviation	Autocorrela- tion Order1	Signal-to-Noise Ratio
S01	C	0.41	0.42	0.43	-
	I	0.40	0.42	0.46	-
	A	0.40	0.42	0.47	22.8
S08	C	0.39	0.43	0.45	-
	I	0.35	0.40	0.45	-
	A	0.36	0.39	0.39	27.3
S11	C	0.35	0.38	0.47	-
	I	0.33	0.37	0.48	-
	A	0.35	0.36	0.39	29.2
S29	C	0.31	0.37	0.52	-
	I	0.24	0.29	0.50	-
	A	0.24	0.28	0.45	8.9

zero. Thus, the divisor used for the index of the CORRIDOR method is smaller making the range of variability larger. The chronology with the weakest climatic signal (South Urals) has the greatest differences in mean sensitivity and standard deviation.

First order autocorrelation values are practically the same in the chronologies developed by the CORRIDOR and INDEX methods. These statistics are lower for three of the ARSTAN chronologies and higher for one chronology. These differences probably reflect the fact that

ARSTAN removes the autocorrelation as it prewhitens the individual tree data, averages the prewhitened data and then adds the average autocorrelation for the trees to obtain the ARSTAN chronology while the other two methods ignore the autocorrelation.

The correlations between the developed chronologies are very high (from 0.917 to 0.981) (Table 3). This indicates that the tree-ring chronologies developed by the three standardization methods are very similar. The differences between the correlations of the CORRIDOR

Table 3. Correlation coefficient values between the tree-ring chronologies developed by various standardization methods

Province	Polar Urals		Subpolar Urals		North Urals		South Urals	
Series Code	S01		S08		S11		S29	
Standardization Method	INDEX	ARSTAN	INDEX	ARSTAN	INDEX	ARSTAN	INDEX	ARSTAN
CORRIDOR	0.960	0.965	0.950	0.937	0.955	0.932	0.917	0.928
INDEX	-	0.951	-	0.966	-	0.965	-	0.981

chronologies with the other two methods decrease slightly in the direction from the Polar to South Urals. However, the correlations between the INDEX and ARSTAN chronologies increase in this direction. A visual comparison of the index plots also shows the high degree of similarity between all chronologies.

The power spectra of the twelve mean chronologies are plotted in Figures 1-4. Each spectrum was computed from 100 lags of the autocorrelation function. The spectral estimates at each wavelength are expressed as percent total variance, and as a continuous distribution of wavelengths throughout the entire spectrum. The spectrum estimates can show the degree of similarity in variance of chronologies at different wavelengths.

The spectra of the Polar Urals chronologies (S01) are almost identical at all frequencies. The INDEX chronology has slightly more variance at the lowest frequencies and the ARSTAN chronology has slightly more variance around 0.05 cycles per year.

The spectra of the Subpolar Urals chronology (S08) show more differences, although they are very similar especially for the INDEX and CORRIDOR chronologies. The ARSTAN method appears to have removed more variance at very low frequencies.

The spectra of the North Urals chronologies (Fig. 3) are also similar with some variations at low frequencies. Somewhat different peaks are significant and the CORRIDOR chronology has the highest variance of the three at 0.005 cycles per year. Fig. 4 for the South Urals shows the same significant peaks, but as noted in Fig. 3, the CORRIDOR chronology had the most variance at the very lowest frequencies.

The three standardizing methods produce chronologies with very similar spectra. Differences can be noted only at frequencies of 0.05 cycles per year or less. Sometimes the CORRI-

DOR method preserves somewhat more low-frequency variation, but the differences may not be large enough to be significant. This difference seemed to be more apparent in the chronologies that contained a weak climatic signal (S29).

The coherence spectra estimate the similarities in variance of two chronologies expressed as the percent agreement (coherence square) at different frequencies (Figs. 5-8). All spectra confirm the high agreement among the chronologies at all frequencies. Most of the estimates exceed the 95% significance level (coherency = 0.93). Occasionally, some estimates at higher frequencies were markedly low and insignificant (Figs. 5-7) due to chance or to a small percent variance in the estimate at that particular frequency (Fig. 1-3).

As was noted for the power spectra, the greatest differences were at the lowest frequencies. The coherence at low frequencies for the Polar Urals is highest for the CORRIDOR-ARSTAN comparison (Fig. 5); it is not so high for the other three areas, but the lack of agreement is often at frequencies with little variance (Figs. 2-4). The phase angle plots for all series indicated that there is no evidence of any lag problems with these data.

We conclude that the tree-ring chronologies developed by the CORRIDOR method and the INDEX and ARSTAN programs are very similar and statistically indistinguishable. Any of the three methods can be used and the results compared to the others without restandardizing. If it is necessary to preserve the very lowest frequencies, the CORRIDOR method may be superior. The ARSTAN method may be the most practical method to use because it can be altered to remove the variance at different frequencies.

However, the ARSTAN program is rather complex and it should be used with care as the available options allow one to alter the fre-

quency distribution markedly. The INDEX program is less flexible, simpler to operate, and tends to have more variance at low frequencies than the ARSTAN program. This may arise from the fact that the exponential function estimated by the INDEX program is better fit to the early portions of the chronology with the most ring-width variability than to the late portions. This creates more error variance and low-frequency trends in the outer part of the chronology. This low-frequency error can be reduced to some extent by the double detrending option of ARSTAN (Holmes et al., 1986). A follow-up study of this phenomenon has been conducted by Fritts and Holmes but this will be the topic of another paper.

Literature Cited

- Blackman, R.B., and J.W. Tukey. 1958. *The Measurement of Power Spectra*. Dover Publications, New York.
- Cook, E.R. 1985. *A time-series analysis approach to tree-ring standardization*. Ph.D. Dissertation, Department of Geosciences, University of Arizona, Tucson, 175 pp.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, London, 567 pp.
- Graybill, D.A. 1982. Chronology development and analysis, pp. 21-30, In Hughes, M.K., P.M. Kelly, J.R. Pilcher, and V.C. LaMarche (ed.s), *Climate From Tree Rings*. Cambridge University Press, Cambridge.
- Holmes, R.L., R.K. Adams, and H.C. Fritts. 1986. *Tree-ring chronologies of Western North America: California, Eastern Oregon and Northern Great Basin with procedures used in the chronology development work including users manuals for computer programs COFECHA and ARSTAN*. University of Arizona, Tucson, Arizona, 182 pp.
- Shiyatov, S.G. 1972. Dendrochronological study of *Picea obovata* in the Lower Taz River, pp. 76-81, In *Dendroclimatology and Radiocarbon*. Kaunas. (In Russian)
- Shiyatov, S.G. 1986. *Dendrochronology of the upper timberline in the Urals*. Moscow: Nauka, 136 pp. (In Russian)

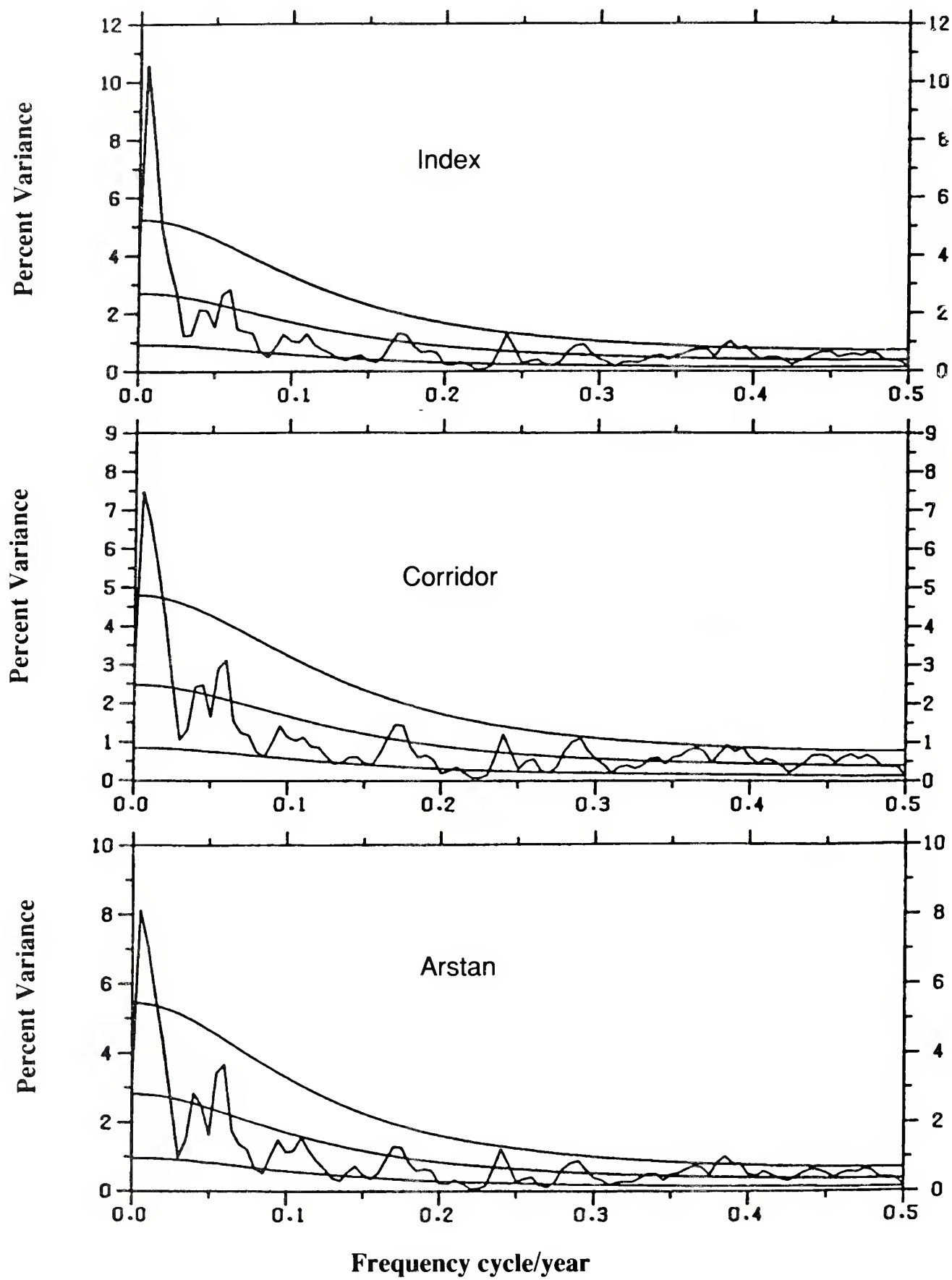


Figure 1. Polar Urals Chronology S01 Comparison of Percent Variance, Period: 1550 to 1968 with 100 Lags

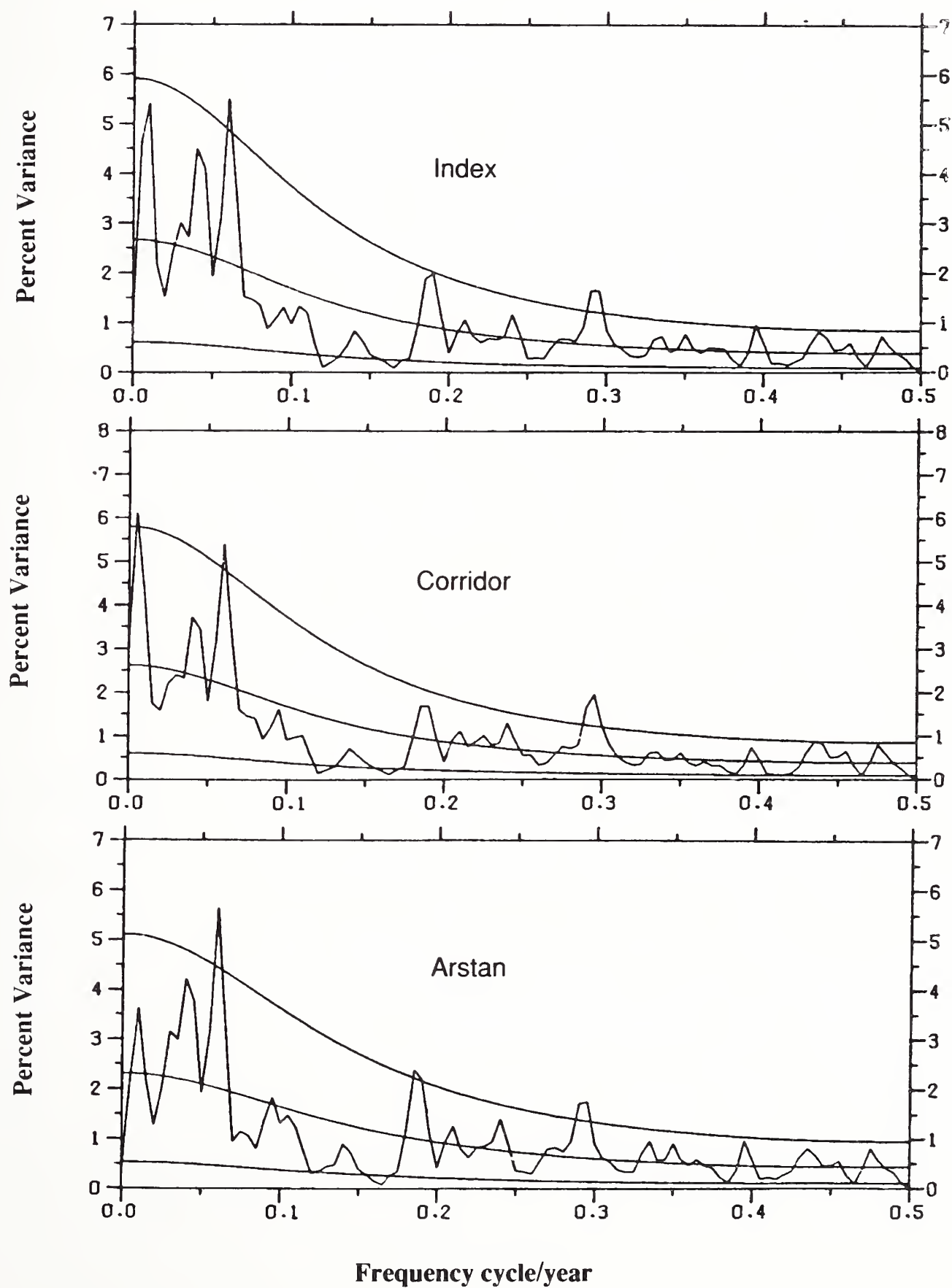


Figure 2. Subpolar Urals Chronology S08, Comparison of Percent Variance, Period: 1691 to 1968 with 100 Lags

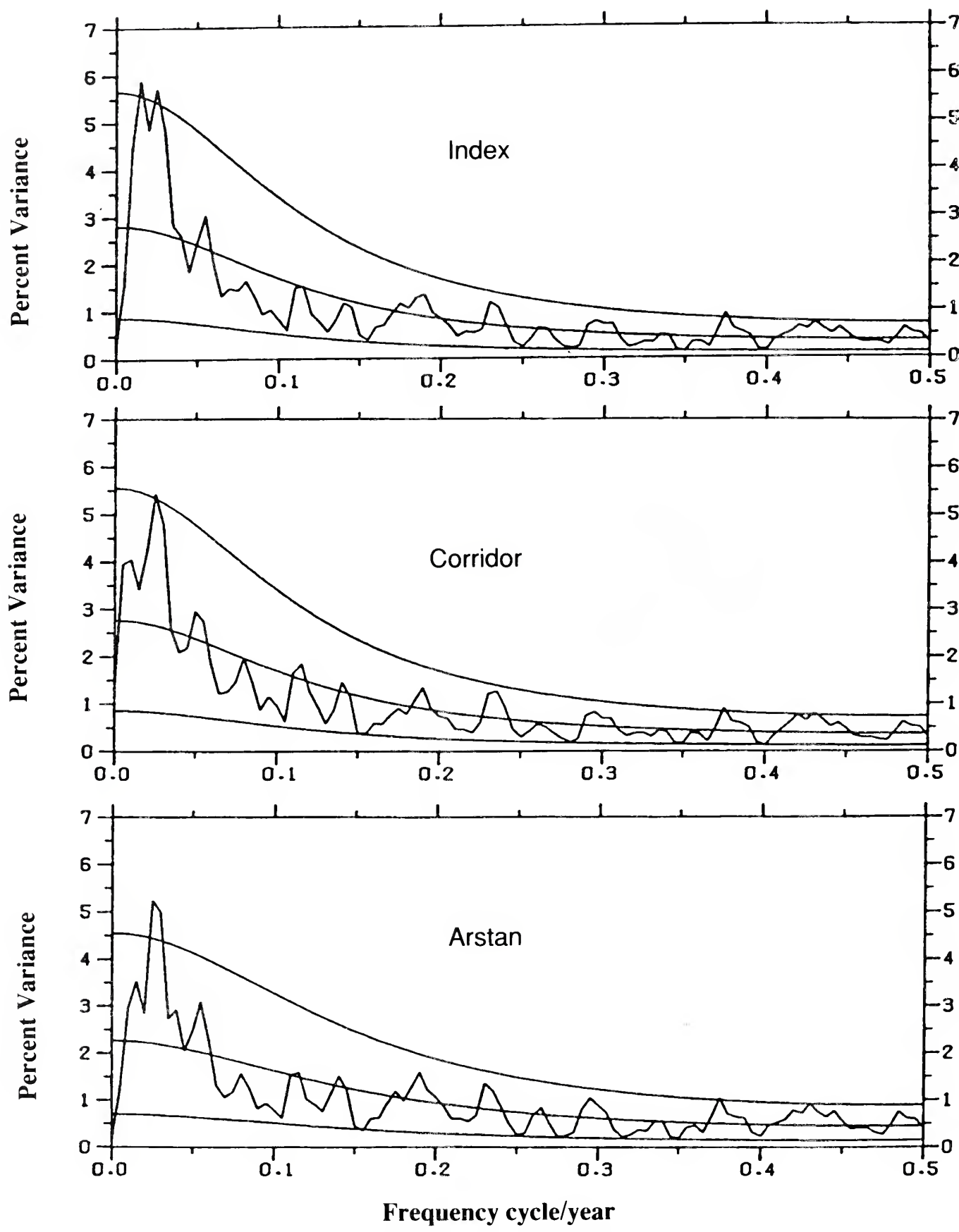


Figure 3. North Urals Chronology S11, Comparison of Percent Variance, Period: 1590 to 1969 with 100 Lags

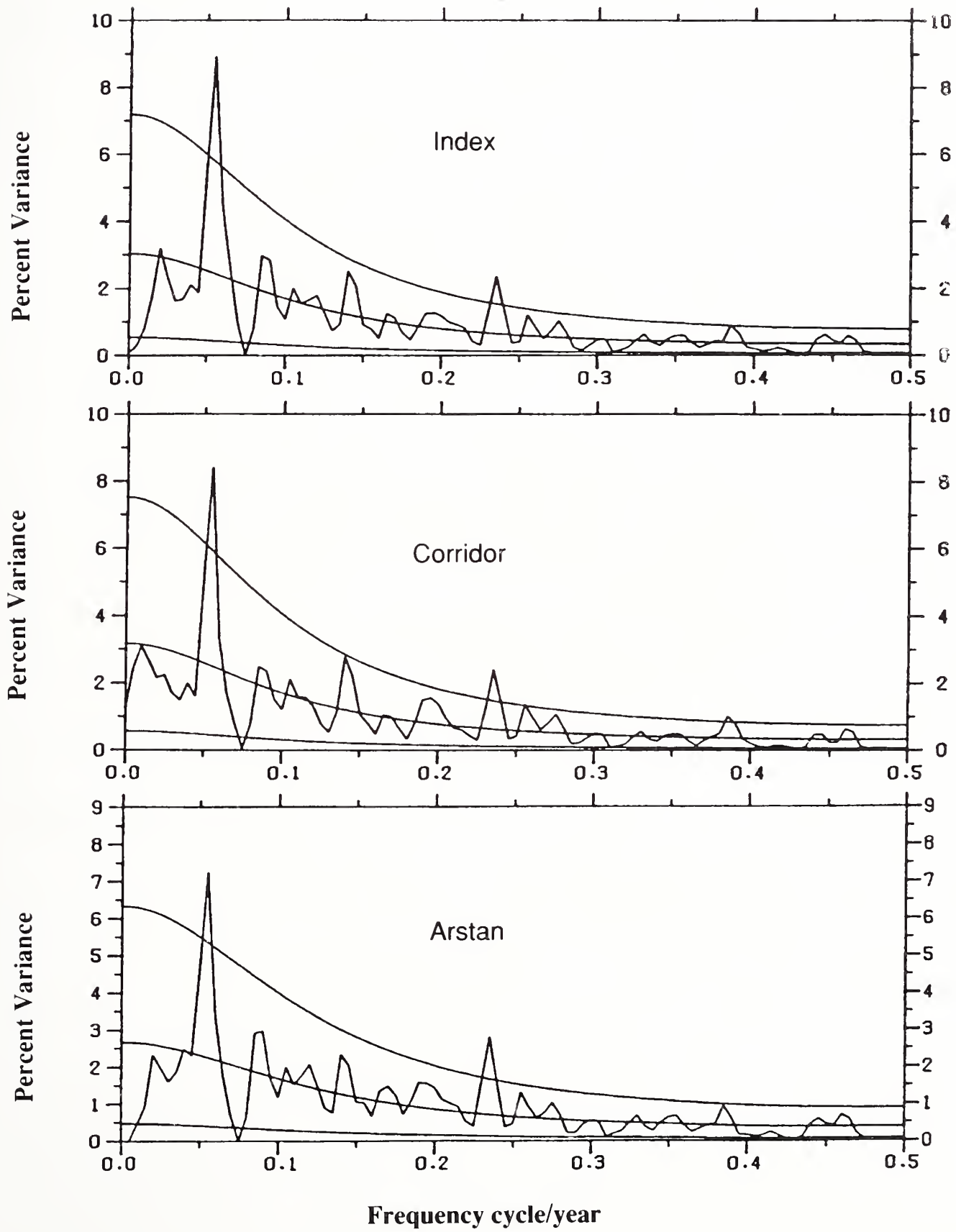


Figure 4. South Urals Chronology S29, Comparison of Percent Variance, Period: 1770 to 1972 with 100 Lags

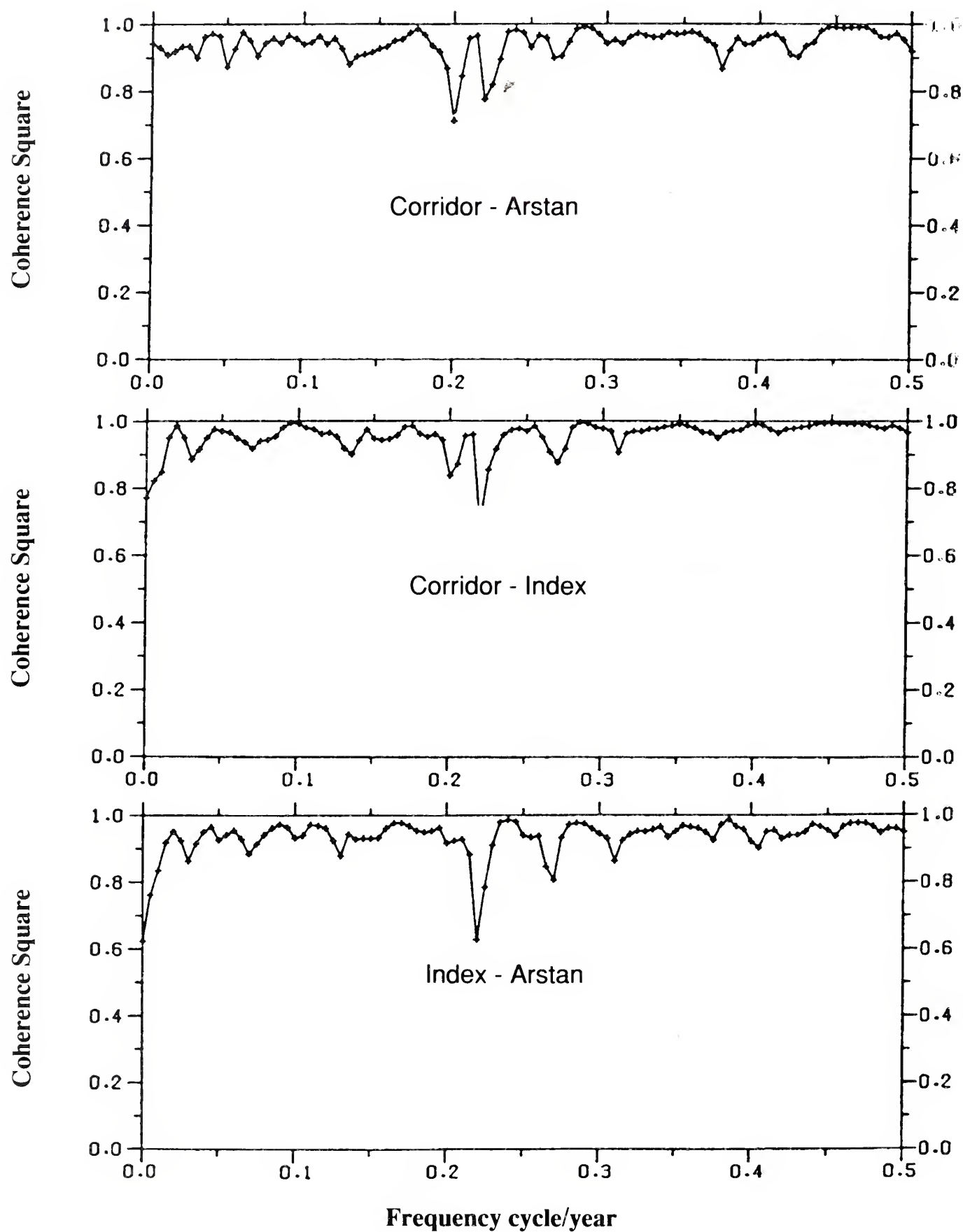


Figure 5. Polar Urals Chronology S01, Comparison of Coherence Square, Period: 1550 to 1968 with 100 Lags

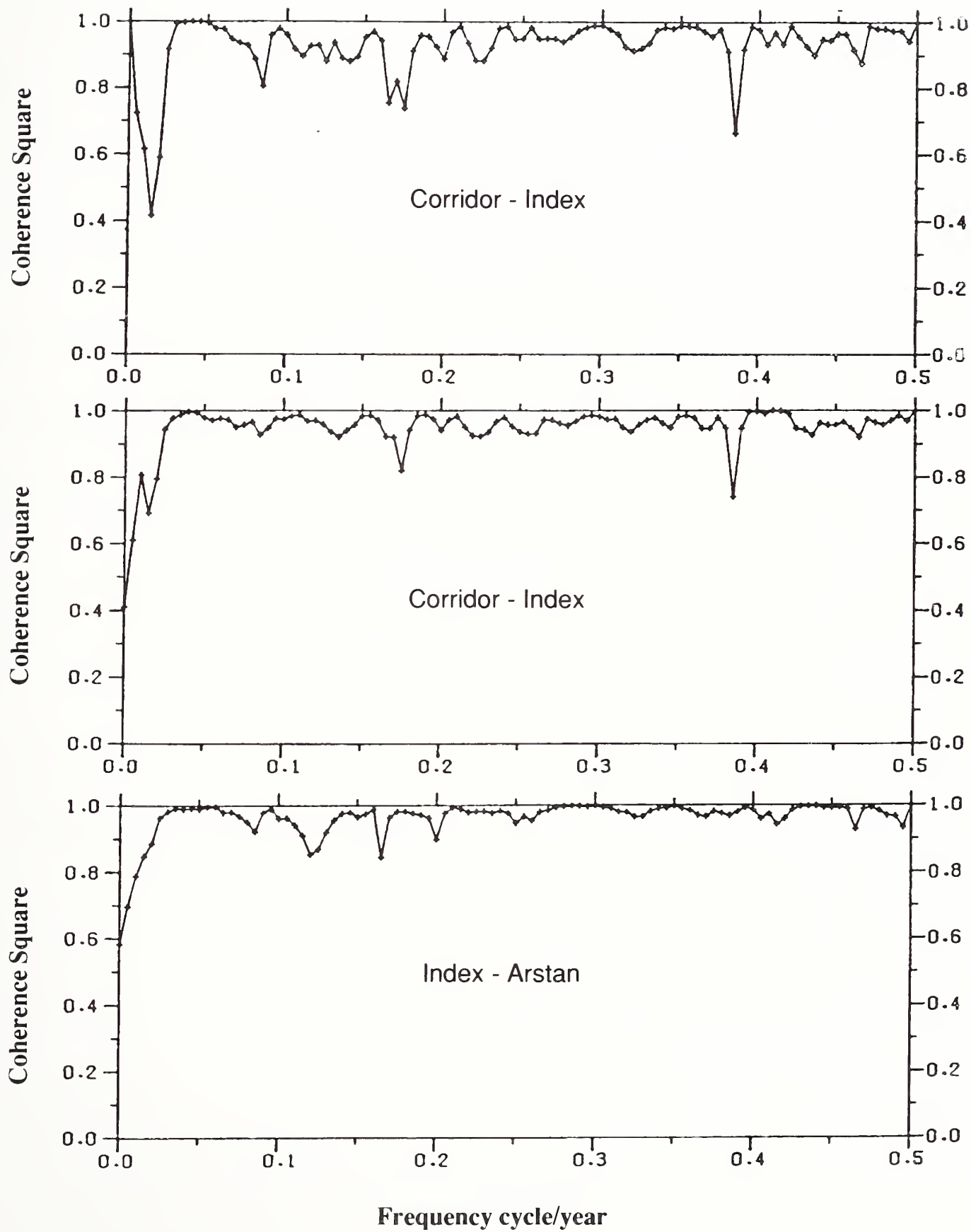


Figure 6. Subpolar Urals Chronology S08, Comparison of Coherence Square, Period: 1691 to 1968 with 100 Lags

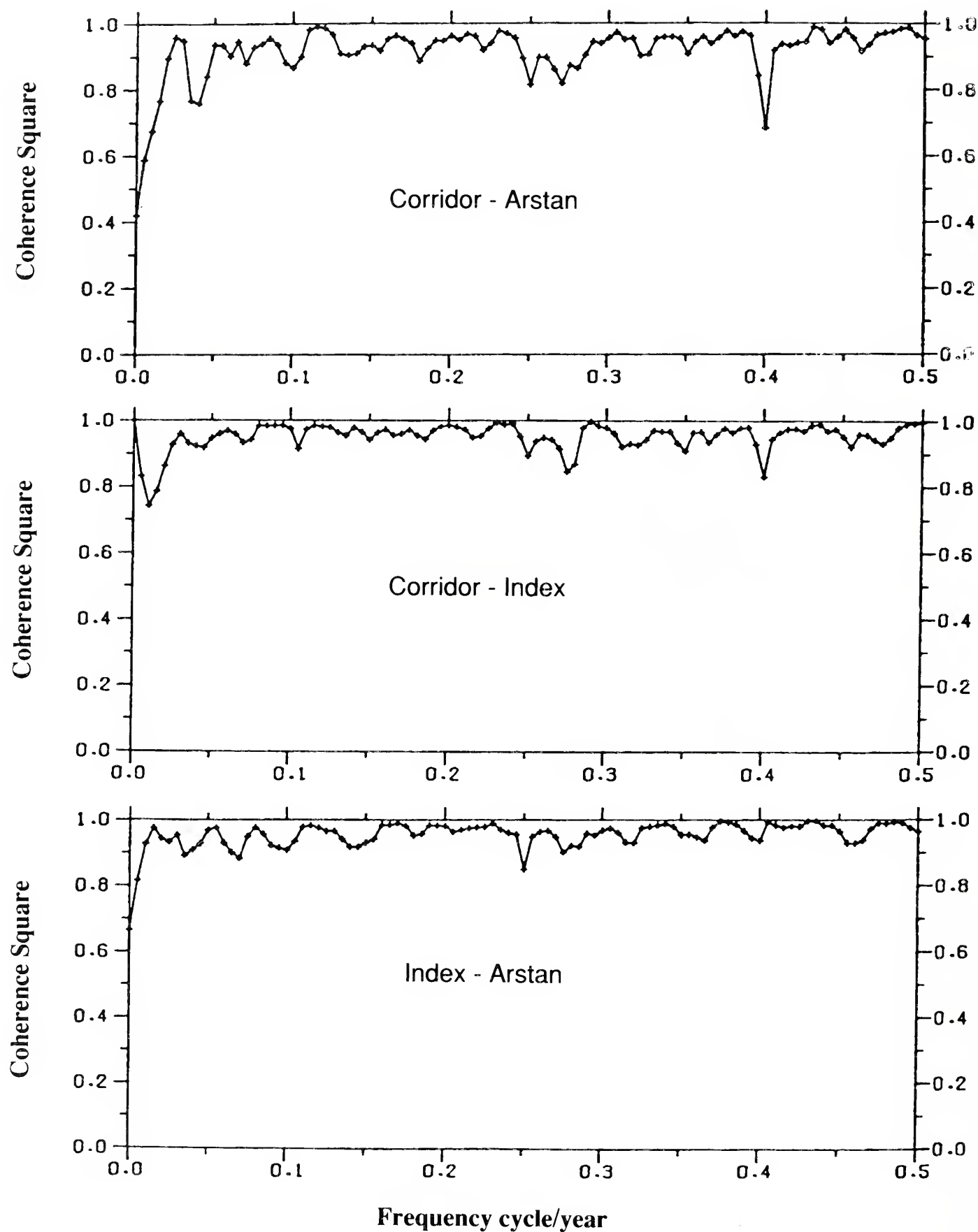


Figure 7. North Urals Chronology S11, Comparison of Coherence Square, Period: 1590 to 1969 with 100 Lags

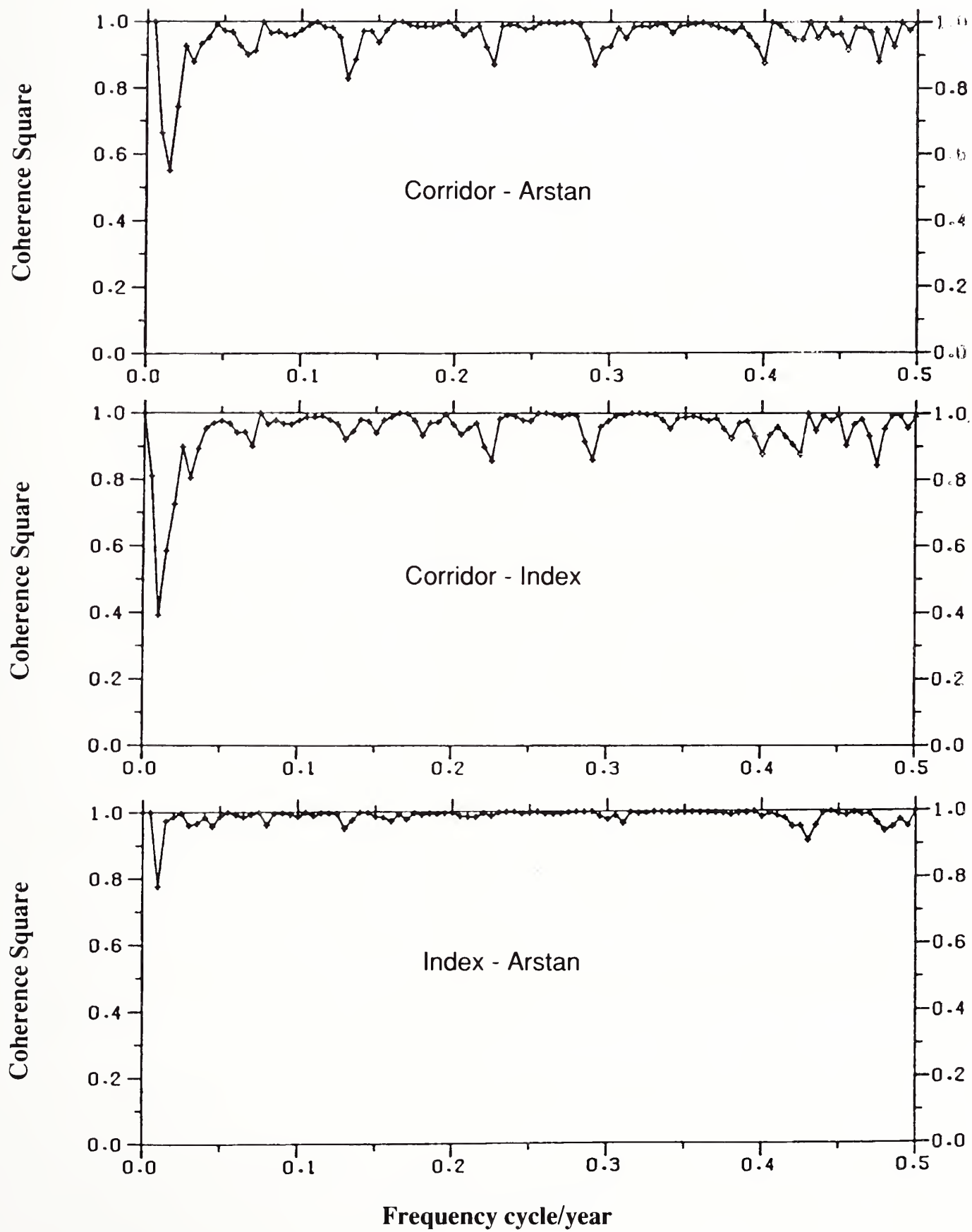


Figure 8. South Urals Chronology S29, Comparison of Coherence Square, Period: 1770 to 1972 with 100 Lags

Spatial Patterns of Climatic Response for Eastern Hemlock and the Potential Impact of Future Climatic Change

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Abstract

The empirical climatic response of eastern hemlock is modeled over most of its geographic range using tree-ring analysis. The structure of the temperature response shows broad spatial coherence from Wisconsin to New England indicating a genetics- and/or habitat-based predisposition to respond to climate in a predictable way. Prior July and current March temperatures are the most important variables followed by current June rainfall. These climate variables increase in importance as the northern and western range limits of hemlock are approached. This suggests that they are influential in determining the distribution of hemlock in those regions. Should future climatic changes affect these influential months, hemlock distribution along the northern and western limits of its range may change accordingly.

Introduction

By the middle of the next century, significant global climatic change is expected from warming caused by increased CO₂ in the atmosphere (Manabe and Wetherald, 1980). Although the regional patterns of CO₂-induced climatic change are uncertain (Schlesinger and Mitchell, 1985),

both general circulation model estimates (Mitchell, 1983) and climatic scenarios (Wigley *et al.*, 1980) indicate that eastern North America will be significantly affected.

These climatic changes should have a large impact on the deciduous/evergreen forests of this region. Vegetation/climate classification schemes (Emanuel *et al.*, 1985) and forest stand simulations (Solomon, 1986) suggest that there will be substantial changes in the range limits of many tree species, concomitant changes in species composition and importance in forest communities, and, for some areas, significant declines in live tree biomass. If these studies are correct, the ecological consequences will be enormous.

To predict how the eastern deciduous forests will be altered by future climatic change, we first need to know how climate presently affects the growth and range limits of the major tree species in these forests. To this end, we have used tree-ring analysis to study the spatial properties of climatic response of eastern hemlock (*Tsuga canadensis* [L.] Carr.), a widely distributed tree species in the eastern deciduous forests.

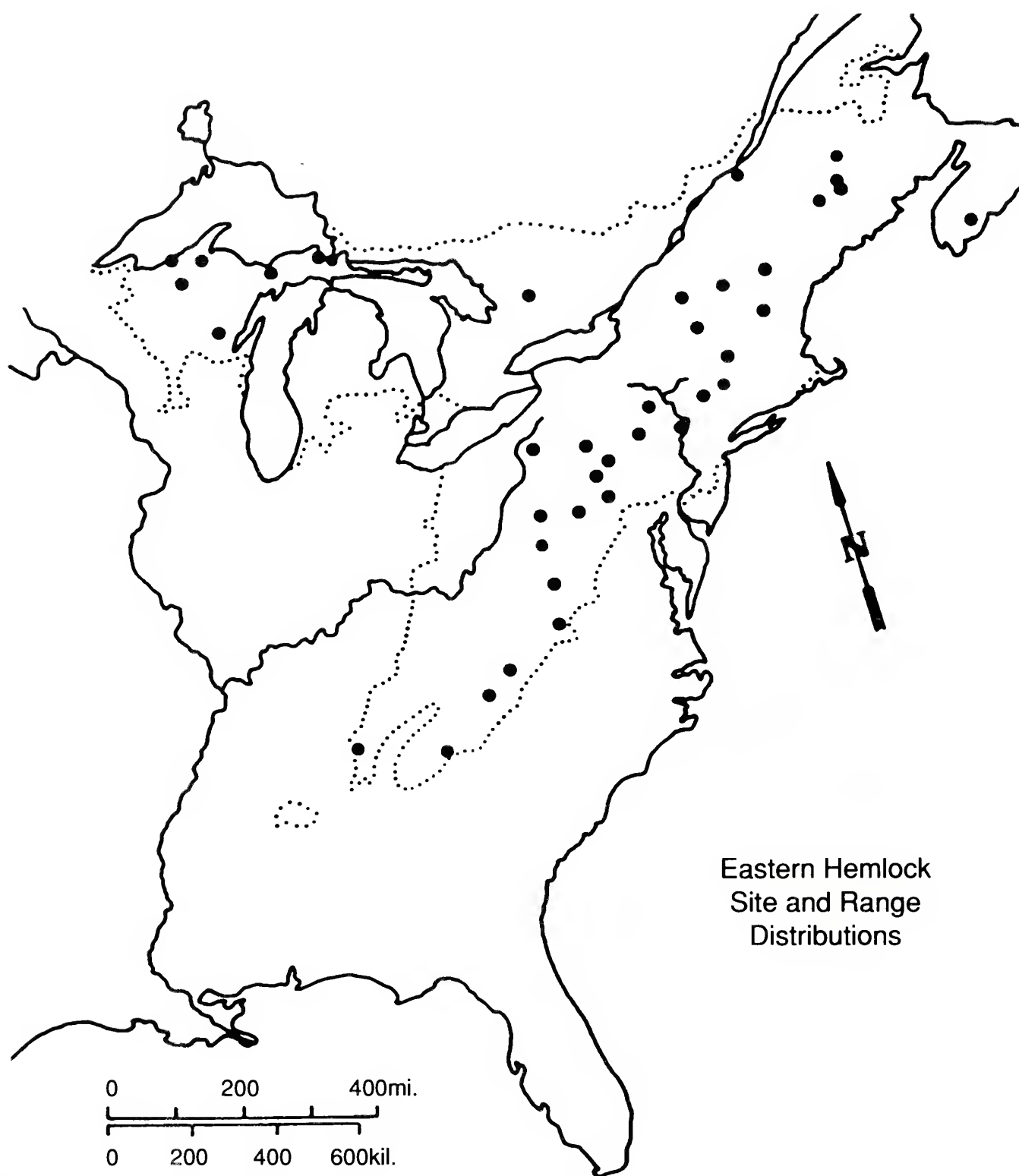


Figure 1. Map of the 42 eastern hemlock tree-ring sites used in this study. Each site is marked by a solid black dot. In some cases, more than one chronology is located at a dot. The range limits of hemlock are shown by the line of small black dots on the map.

Eastern Hemlock

Eastern hemlock is an evergreen tree species native to eastern North America. Its present northern and western range limits (Fig. 1) were reached around 1000-2000 years ago based on pollen evidence (Davis, 1981). The lack of more recent migration suggests that

hemlock is at equilibrium with climate and other factors affecting its distribution (Davis *et al.*, 1986).

Hemlock typically grows in cool, humid environments where adequate soil moisture is usually available. It is one of the most shade-tolerant tree species (Fowells, 1965) and can

grow for decades as a suppressed understory tree before attaining canopy status. The foliage of eastern hemlock is extremely dense, allowing little light to penetrate to the forest floor. Thus, the environment beneath a well-developed hemlock canopy is cooler and damper than that found under hardwood canopies in the same region (Fowells, 1965).

How much climate determines the range of eastern hemlock is difficult to infer from the available studies of the species. In the Great Lakes region, Davis (1981) suggests that the halt of hemlock migration south of Lake Michigan about 6000 years ago was due to excessive dryness in the Midwest. Solomon (1986) uses a minimum growing degree day (GDD) isotherm of 1324 GDD as the potential northern range limit. This isotherm approximates the present northern boundary of the species. However, Kavanagh and Kellman (1986) propose that competition is more important than temperature due to the preference of hemlock for northerly and westerly facing slopes. In the Southern Appalachians and for disjunct stands in the Midwest, hemlock is probably limited more by the existence of suitable microhabitats controlled by physiography than by any special set of macroclimatic variables (Fowells, 1965). Thus, the range limit of hemlock in the Midwest is probably determined by drought frequency and the existence of suitable microhabitats, but the importance of climate in determining the northern range limit is less clear.

Over the past several years, 42 annual tree-ring chronologies (Fritts, 1976) have been developed for eastern hemlock over most of its natural range (Fig. 1). All of the chronologies are mean-value functions of cross-dated and standardized ring-width series from 15 to 30 trees in a stand. These chronologies were originally developed for reconstructing past climate from tree rings, and all are at least 262 years in length. Although the stands are not a true random sample, there was no selectivity in choosing sites having defined intrinsic characteristics

such as slope aspect, soil type, or elevation. Rather, the principal criterion for site selection was that the stand was "old-growth."

Prior to statistical analysis, the hemlock chronologies were prewhitened with autoregressive models (Box and Jenkins, 1970) to remove autocorrelation due largely to internal biological processes of the trees and unique stand characteristics and histories. The prewhitened chronologies have the advantage of being cleaner reflections of the original environmental inputs that affect tree growth. In addition, the lack of autocorrelation greatly simplifies statistical significance tests between tree rings and climate.

Spatial Properties of Eastern Hemlock Tree Rings

To determine if some potentially useful spatial information was contained in the tree-ring data, principal components analysis (PCA) with analytical rotation (Richman, 1986) was applied to the 42 chronologies for 207 years covering the time period 1770-1976. We conjectured that if no reasonably coherent spatial patterns were found in the tree-ring data, then local (i.e. microclimatic and nonclimatic) influences would probably be the dominant source of variance in the chronologies. If so, the search for macroclimatic controls on hemlock growth and distribution would probably be futile.

PCA was applied to the correlation matrix of the chronologies. The first 6 factors had eigenvalues greater than 1.0, which explained 66 percent of the total variance. These factors were then analytically rotated using Harris-Kaiser oblique rotation (Richman, 1986). Figure 2 shows the maps of these hemlock spatial factors. Only regions with sites having factor loadings ≥ 0.60 have been contoured. The square of the factor loading can be interpreted as the percent variance in common between the original variable and the particular factor. Thus,

loadings of 0.70 indicate ~50 percent variance in common between the variable and the factor. The factors show very clear geographic patterns, which is strong evidence for some macro-environmental influences on hemlock growth in eastern North America.

From these results, we hypothesized that the observed spatial structure could be caused by two different, but not necessarily exclusive, phenomena. These were:

1) The factor patterns were caused by inherent regional patterns of climate that are independent of hemlocks's response to climate. If this were the case, then the climatic response models may be similar both within and between the factor regions. A similar climatic response between factors would argue for a genetics- and/or habitat-based predisposition of hemlock to respond to climate in a specific way.

2) The factor patterns were caused by geographic dependence in the climatic response of hemlock. If this were so, then the climatic response models of hemlock should be the same within each geographic factor, but different between factors. This condition would argue for climate exerting a more local control on hemlock distribution with different sets of limiting factors controlling growth in each factor region.

These two hypotheses will be discussed in the next section where the spatial properties of climatic response by eastern hemlock will be examined.

Spatial Patterns of Climatic Response in Eastern Hemlock

Monthly temperature and precipitation records (Boden, 1987; Bradley *et al.*, 1985) were used to model the climatic response of eastern hemlock. Although these meteorological variables are not perfect surrogates for the true macroclimatic inputs affecting hemlock growth, they are the only ones available with the

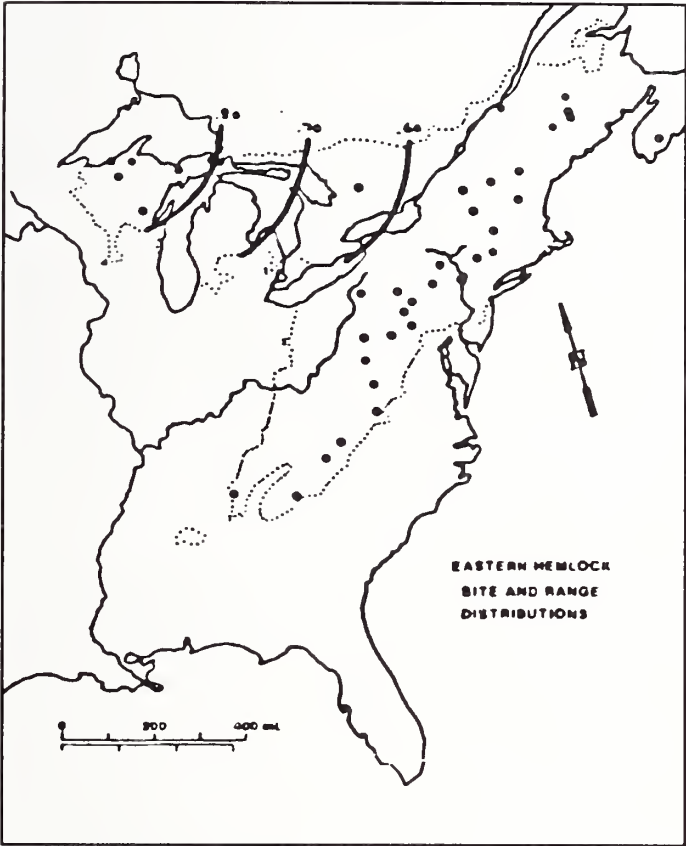
necessary spatial and temporal coverage.

We used a "nearest neighbor" approach in pairing meteorological station records with the tree-ring chronologies. In most cases, we were able to use unique pairs of chronologies and station records. However, in some areas like Maine, the small number of suitably located meteorological stations forced us to use the same climatic data for several chronologies. This reduced the number of unique pairs to 36 or 85.7% of the total number of chronologies.

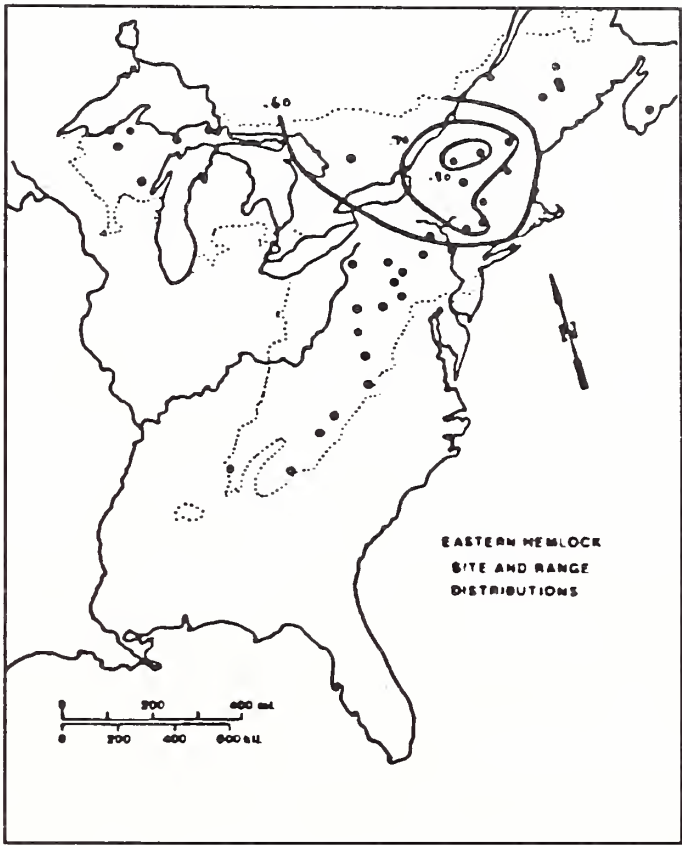
The product-moment correlation coefficient was used to characterize the climatic response of hemlock. This method does not offer any predictive capability in the sense of regression analysis. However, the information gleaned from correlation analysis will be useful in constructing future regression-based response models.

A dendroclimatic year beginning in May of the previous year and ending in September of the current year of growth was used in the correlation analyses. This 17-month year includes two radial growth seasons and the intervening cold season months when climatically induced physiological preconditioning can occur (Fritts, 1976). The simple correlations were computed for the 1931-1976 period. This time period was chosen because one station begins in 1929, and the data not used from the other stations will allow us to validate the regression-based models to be developed in the future. With these degrees-of-freedom ($df=44$), any correlation $>|\pm 0.30|$ ($p<0.05$) is potentially meaningful.

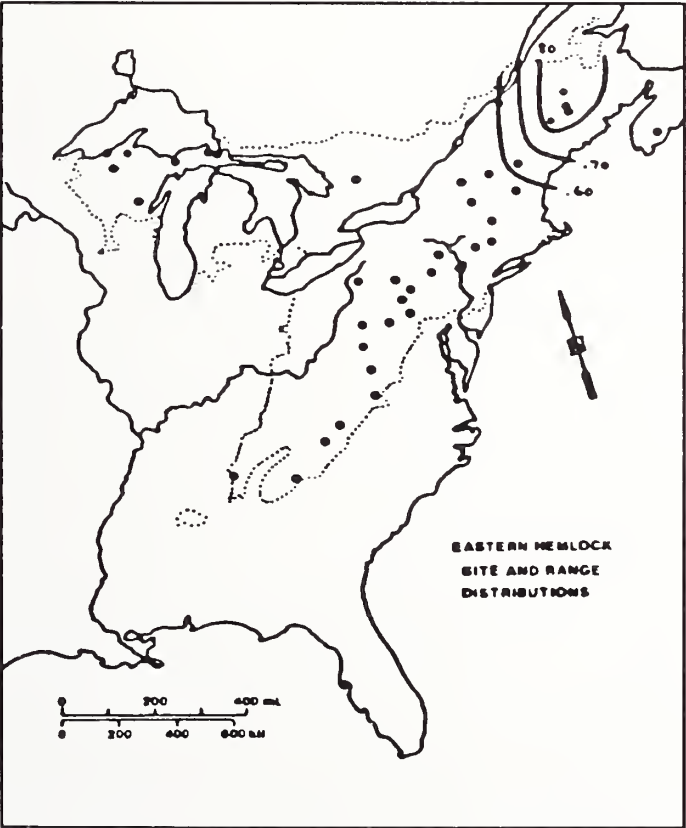
The temperature analyses revealed spatially coherent patterns of negative correlation for the prior July (22 out of 42 <-0.30) and positive correlation for March of the current growth year (27 out of 42 $>+0.30$). These significant correlations are especially apparent for sites in the central and northern parts of the range (Figs. 3A & B) where the correlations are highest. Significantly, the consistency of the



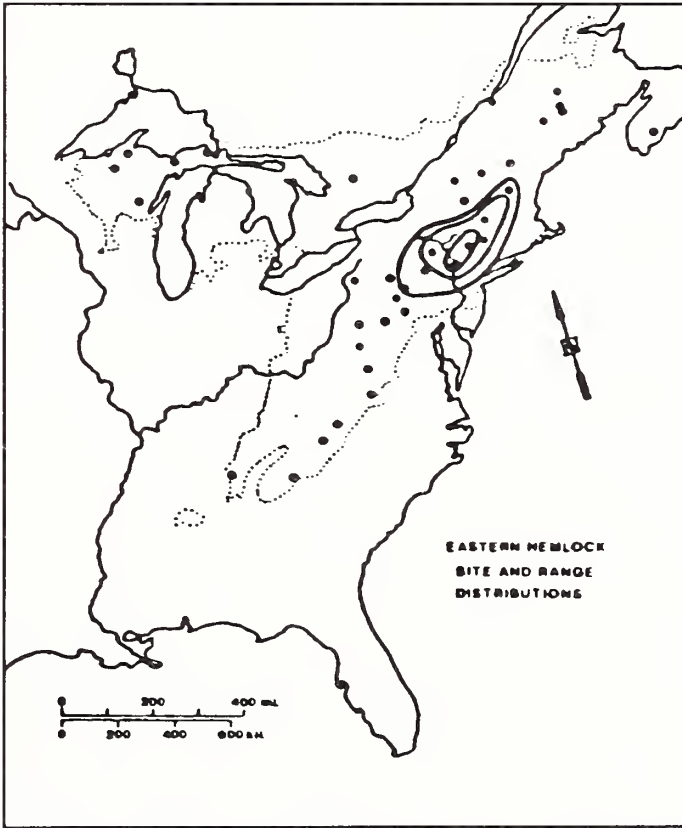
GREAT LAKES FACTOR



NEW YORK -NEW ENGLAND FACTOR

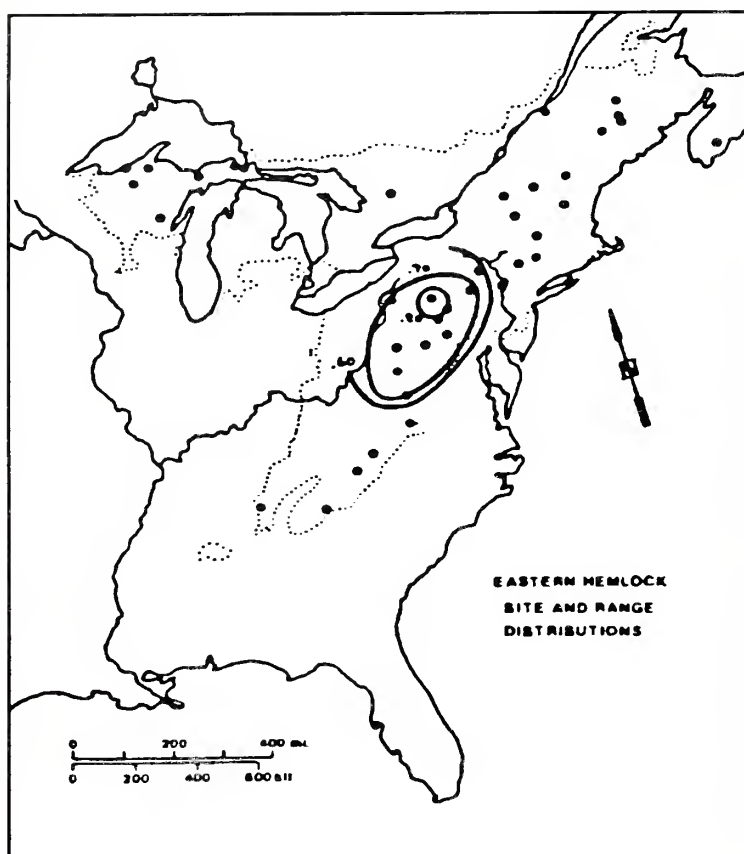


MAINE FACTOR

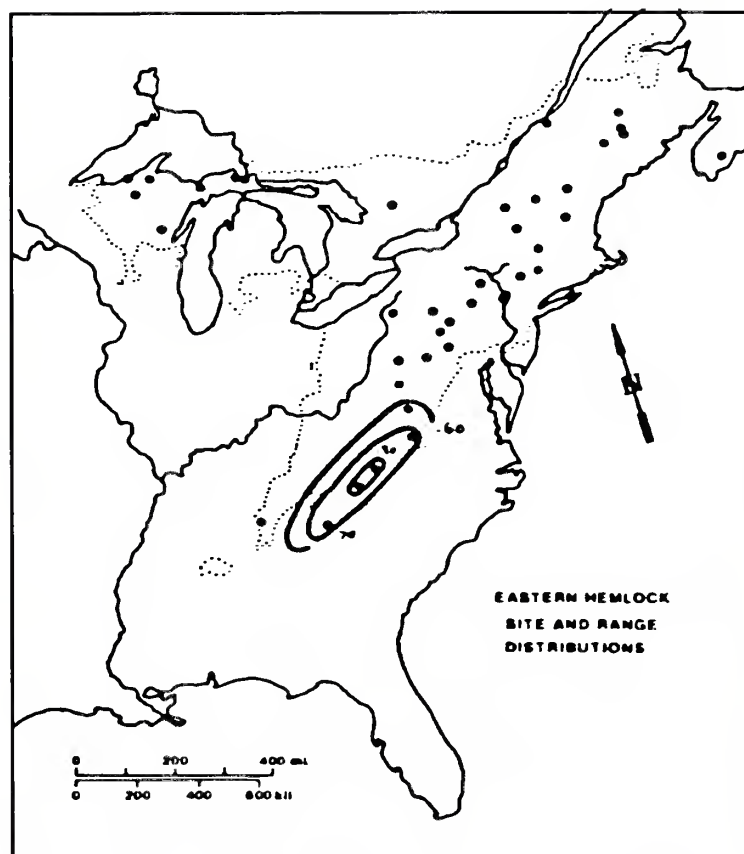


SOUTHEASTERN NEW YORK-EASTERN PENNSYLVANIA FACTOR

Figure 2. The eastern hemlock spatial factors based on tree rings.



PENNSYLVANIA-NORTHERN VIRGINIA
FACTOR



SOUTHERN APPALACHIAN FACTOR

Figure 2. The eastern hemlock spatial factors based on tree rings (continued).

July and March temperature correlations extends across the spatial factors in Fig. 2. This suggests that hypothesis #1 is largely correct. That is, eastern hemlock is predisposed by genetics and/or habitat to respond to temperature in a similar way over much of its range. This finding is also consistent with Fowells (1965) who noted the similarity of the microclimate in hemlock stands over wide geographic areas.

The results of the precipitation analyses were less successful. Only one weak geographic pattern was indicated for June of the current growth year (5 out of 42 $>+.30$). However, the pattern of these correlations (Fig. 3C) indicates that the importance of June rainfall increases as the northwestern range limit is approached. The weakness of the precipitation results may be due, in part, to using single station records instead of regionally averaged records, which have been shown to be better correlated with tree rings (Blasing *et al.*, 1981).

To examine the spatial consistency of the overall monthly temperature response, we subjected the full suite of correlations to PCA with analytical rotation. In this case, the first two eigenvalues explained 75 percent of the variance, with eigenvalue #1 accounting for the most at 62 percent. This indicates that the pattern of correlations between hemlocks and monthly temperatures are also much more spatially consistent than the patterns in the tree rings themselves. After the two eigenvectors were obliquely rotated, an extremely broad northern temperature response emerged, followed by a more southerly Pennsylvania-Northern Virginia response (Fig. 4). The Southern Appalachian hemlock sites are not represented in either factor probably because of greater heterogeneity in the temperature response patterns seen there and because of the relatively small number of sites from that region. The monthly factor scores of these patterns (Fig. 5) are extremely similar, with a correlation

of 0.98. Thus, the existence of different spatial patterns of temperature response is questionable. The only apparent difference in the scores is a slightly higher emphasis on prior June temperature in the more southerly factor #2. There is some indication that November and February temperatures also have a weak influence on hemlock growth when viewed across the region, even though on a site-specific basis they are rarely statistically significant.

Discussion

The results of this study indicate that eastern hemlock is strongly and predictably

influenced by climate in a broad geographic way. There is effectively only one pattern of temperature response in the tree-ring chronologies studied here, with the exception of the Central and Southern Appalachian sites. Therefore, the existence of 6 spatial tree-ring patterns can be largely explained by the regionality of climate, not by regional differences in hemlock's response to climate. The exceptions to this conclusion are the Central and Southern Appalachian sites and, to a lesser degree, the Maine sites. While the monthly structure of the temperature response is spatially stable over a very large part of hemlock's range, the magnitudes of the correlations show distinct geo-

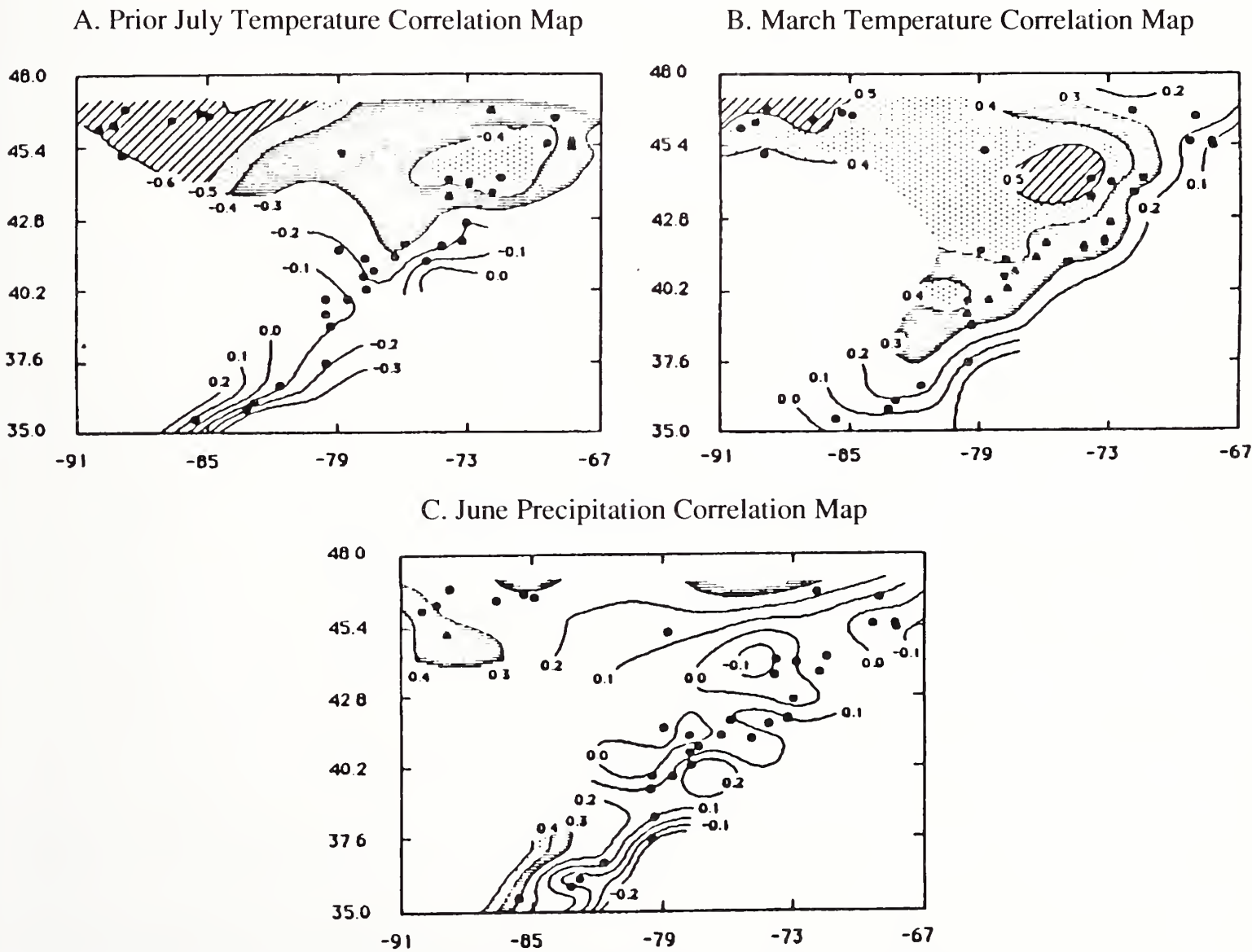
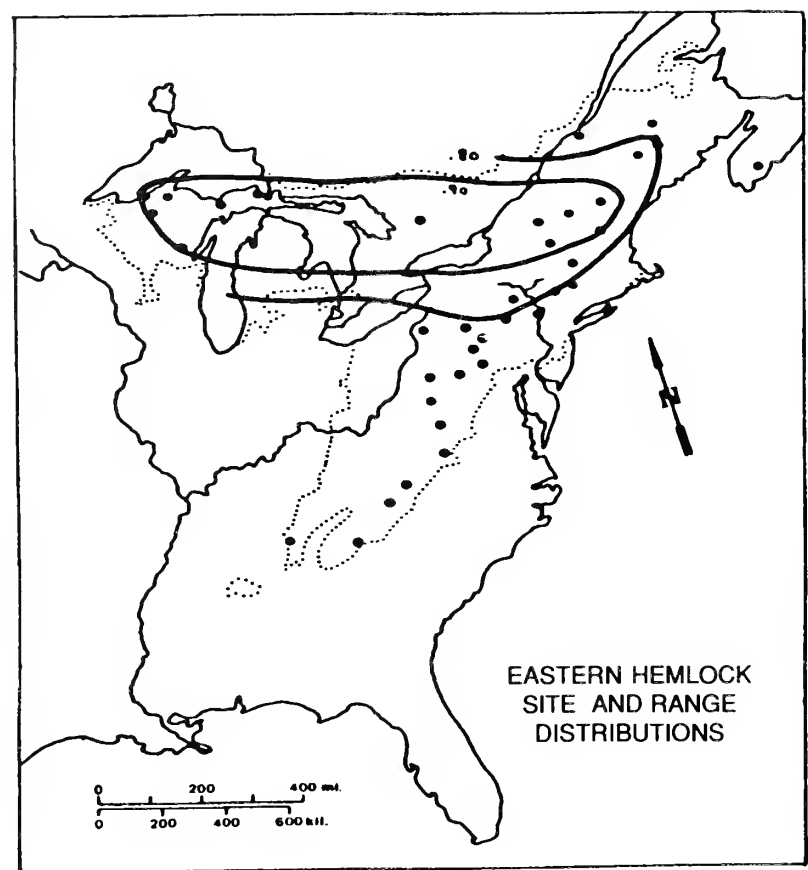
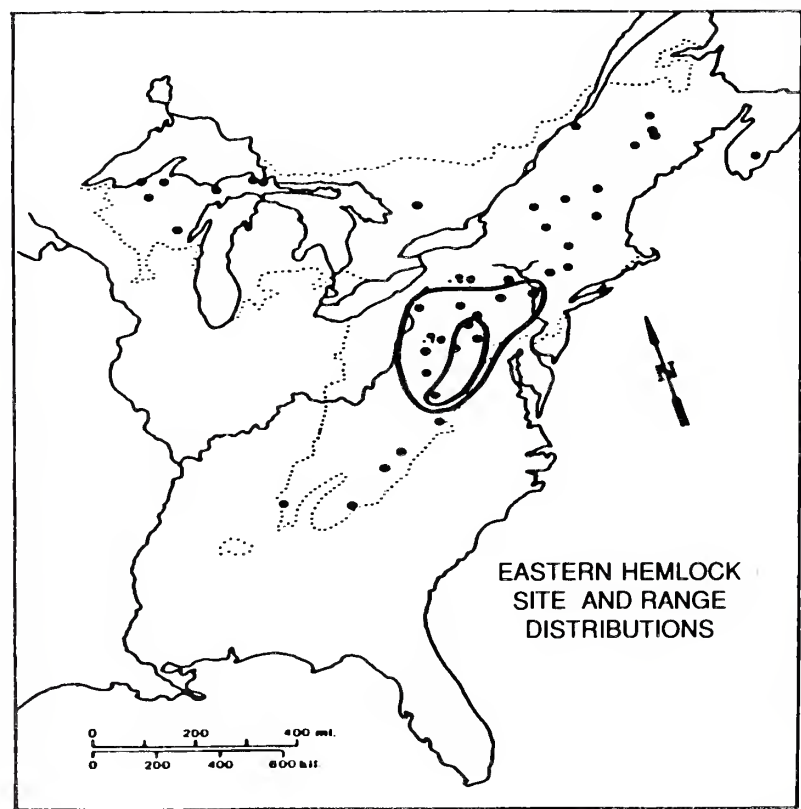


Figure 3. Contoured maps of the correlations between the 42 hemlock chronologies and prior July (A) temperature, March (B) temperature, and June (C) precipitation. The maps have been smoothed and contoured using distance-weighted least squares. Only those contours exceeding ± 0.30 are shaded. The solid black dots denote the locations of the tree-ring sites.



TEMPERATURE FACTOR PATTERN #1



TEMPERATURE FACTOR PATTERN #2

Figure 4. The spatial patterns of temperature response for eastern hemlock.

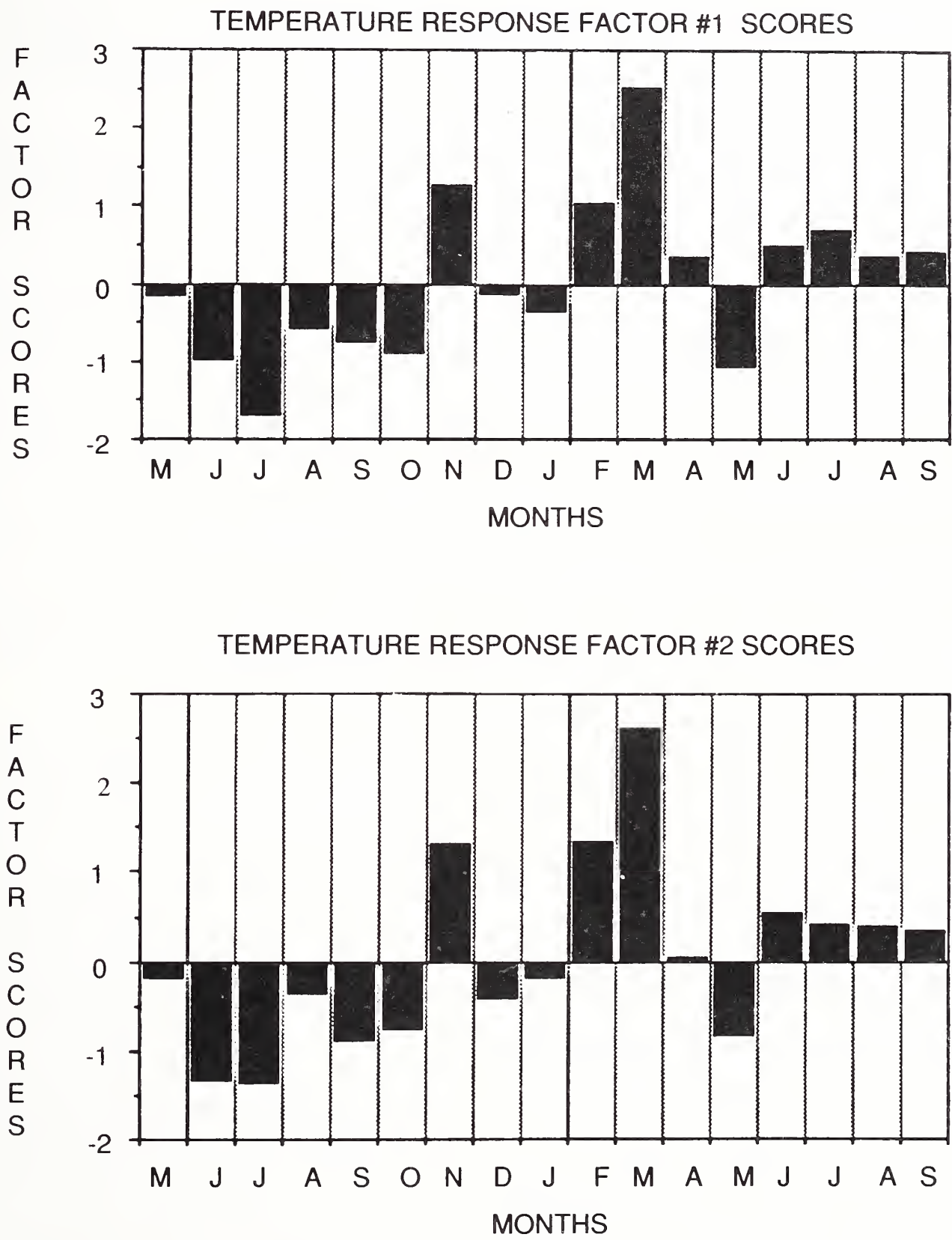


Figure 5. The factor scores of the two principal temperature factors for hemlock. The factors, themselves, are shown in Fig. 4.

graphic variations. For July and March, these variations increase as the northern and western range limits are approached. This is especially true for the hemlock sites in the Great Lakes region.

The strong negative correlations between prior July temperatures and hemlock growth in the Great Lakes region argue for this variable being very important in determining the range limits of the species there, probably through its effect on evapotranspiration demand. This sug-

gests that persistent increases in July temperatures coupled with decreases in June rainfall will have a negative effect on hemlock growth, which could ultimately lead to an eastward contraction of its range. The spatially coherent March temperature response was totally unexpected. We cannot say from these analyses how it relates to the northern range limits of hemlock because the physiological basis for the March temperature effect is obscure. However, it is possible that if future climatic change results in warmer March temperatures, then this effect may provide the necessary margin for hemlock to extend its range limits northward.

Acknowledgements

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Literature Cited

- Blasing, T.J., D.N. DuVick, and D.C. West. 1981. Dendroclimatic calibration and verification using regionally averaged and single station precipitation data. *Tree-Ring Bulletin* 41:37-44.
- Boden, T.A. 1987. *United States Historical Climatology Network (HCN) Serial Temperature and Precipitation Data*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Bradley, R.S., P.M. Kelly, P.D. Jones, H.F. Diaz, and G.M. Goodess. 1985. *A Climatic Data Bank For Northern Hemisphere Land Areas, 1851-1980*. Carbon Dioxide Research Division, U.S. Department of Energy, Washington, D.C.
- Box, G.E.P. and G.W. Jenkins. 1970. *Time Series Analysis: Forecasting and Control*. Holden-Day, New York.
- Davis, M.B. 1981. Quaternary history and stability of deciduous forests. In: D.C. West, H.H. Shugart & D.B. Botkin (eds.) *Forest Succession*. Springer-Verlag, New York. pp. 132-177.
- Davis, M.B., K.D. Woods, S.L. Webb, and R.P. Futyma. 1986. Dispersal versus climate: Expansion of *Fagus* and *Tsuga* into the upper Great Lakes region. *Vegetatio* 67:93-103.
- Emanuel, W.R., H.H. Shugart, and M.P. Stevenson. 1985. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Climatic Change* 7:29-43.
- Fowells, H.A. 1965. *Silvics of Forest Trees of the United States*. Agricultural Handbook No. 271, U.S. Department of Agriculture, Washington, D.C.
- Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press, New York.
- Kavanagh, K. and M. Kellman. 1986. Performance of *Tsuga canadensis* (L.) Carr. at the centre and northern edge of its range: a comparison. *Journal of Biogeography* 13:145-157.
- Manabe, S. and R.T. Wetherald. 1980. On the distribution of climate change resulting from an increase in CO₂-content of the atmosphere. *Journal of the Atmospheric Sciences* 37:99-118.
- Mitchell, J.F.B. 1983. The seasonal response of a general circulation model to changes in CO₂ and sea temperatures. *Quarterly Journal of the Royal Meteorological Society* 109:113-152.
- Richman, M.B. 1986. Rotation of principal components. *Journal of Climatology* 6:293-335.
- Schlesinger, M.E. and J.F.B. Mitchell. 1985. *Model projections of the equilibrium climatic response to increased carbon dioxide*. In: M.C. MacCracken and F.M. Luther, eds. U.S. Department of Energy Document DOE/ER-0237. pp. 81-148.
- Solomon, A. 1986. Transient response of forests to CO₂-induced climatic change: simulation modeling experiments in eastern North America. *Oecologia* 68:567-579.
- Wigley, T.M.L., P.D. Jones, and P.M. Kelly. 1980. Scenario for a warm, high-CO₂ world. *Nature* 283:17-21.

A 1009 Year Tree-Ring Reconstruction of Mean June-July Temperature Deviations in the Polar Urals

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We have made a reliable reconstruction of average June-July temperature departures for the period of A.D. 961-1969 using tree-ring width variation of *Larix sibirica* from the north Polar Urals of the USSR. This is the first dendro-chronological reconstruction of seasonal temperature over the past millennium for the sub-Arctic. It is of considerable interest, not only because of its length, but also for the reason that it may contain information about trends and long-term variation in temperature over large areas. The tree-ring chronology (Shiyatov #1-4a, 1986) was developed from ring-width series taken from both living and dead individuals near treeline at elevations of 150-380m just south of the Kara Sea. The region around the Kara Sea is thought to be one that is particularly sensitive to long-term trends and variations in temperature over the Arctic and even the Northern Hemisphere. This is based on an analysis of instrumented values of surface air temperatures for the period of 1881-1980 (Kelly *et al.*, 1982).

Individual tree-ring series were initially crossdated with each other and all rings were assigned calendar years based on the known collection dates of the living series. Ring-widths were measured to the nearest 0.01mm and then each series was treated with the Corridor Method of Standardization (Shiyatov and Mazepa, 1987). Seventy-six of these series were combined by simple averaging to form a tree-ring index chronology for the region.

Changes in the strength of the common signal in chronologies such as these are of interest. As sample size per year decreases, usually near the early part of one, generalizations about the reliability of a reconstruction developed from it during those years may need to be tempered. A useful measure for consideration of this is the Subsample Signal Strength (SSS) (Wigley *et al.*, 1984). This estimates the variance agreement that might be obtained with reduced numbers of a fuller sample of series. It was possible to make an estimate of the SSS with a subset of 13 ring-width index series that

Table 1. Chronology subsample signal strength.

N of series	Variance agreement	First year with this N
1	.69	960
2	.83	1017
3	.89	1018
4	.92	1042
5	.94	1086
6	.96	1089
7	.97	1094
8	.98	1108
9	.98	1141
10	.99	1142
11	.99	1170
12	.99	1172
13	1.00	1190

were included in this chronology during the period of 1800-1960. The results presented in Table 1 also include the earliest years in the chronology where the numbers of series range from one to thirteen. This provides an approximate guide to the reliability of the reconstruction in those early years. The overall strength of the common signal is estimated by two other figures that includes the amount of variance held in common (61 percent) and the signal-to noise ratio (25.8:1). These values are in the uppermost range for chronologies considered to be useful as temperature indicators (Fritts, 1976; Graybill, 1982, 1985; and Wigley *et al.*, 1984).

Instrumented temperature series used in this study are from a monthly mean value data set that is available for the Northern Hemisphere on a grid of 5° latitude by 10° longitude (Jones *et al.*, 1985). These are expressed as departures in degrees celsius from a 1951-1970 normal period. Values for the period of 1881-1969 were selected from the grid point nearest the tree-ring data, latitude 65°N, longitude 70°E.

The relationship between tree growth and monthly mean temperature departures was

investigated with simple correlation procedures. The strongest relationship occurs during the months of June and July, essentially the growing season at this latitude. The correlation for the early summer average of values with the tree-ring series is +0.78 ($p < 0.01$). High positive correlations between ring-width growth and summer temperature have commonly been found in other studies at similar high latitudes. Cooler temperatures apparently limit growth processes while warmer temperatures enhance them. (Jacoby and Cook, 1981; Briffa *et al.*, in press).

Time-series and other statistical characteristics of both data series were evaluated for the purpose of determining their suitability for use in linear regression analysis. Common problems that are encountered in climatic and tree-ring series are non-normality and autocorrelation. For various statistical reasons, neither characteristic is desirable when the series are to be used in Ordinary Least Squares regression (Wonnacott and Wonnacott, 1981). The tree-ring indices are not normally distributed and show moderate but significant persistence. They were prewhitened after an ARMA(1,1) model was found to be the best fit (Box and Jenkins,

1976). The resultant white noise residuals are normally distributed. The temperature series exhibits slight but significant autocorrelation and is normally distributed. This series was, however, not prewhitened due to the limited amount of persistence involved and to uncertainty about the representativeness of this 89 year data set as a realization of the longer term autocorrelation structure.

Several calibration-verification trials using simple linear regression were made to determine how adequately the white noise residuals of the tree-ring indices could predict the temperature departures. The first set of two analyses successively used one half of the data over

the period of 1882-1969 for calibration and the other half for verification. A set of three trials successively used two-thirds of the data for calibration and the remaining one-third for verification. A set of four trials was conducted in a similar fashion. Results of these trials were acceptable in terms of the evaluation of standard goodness-of-fit criteria, and in terms of the characteristics of the regression residuals. The results of several associated tests commonly used in dendroclimatic research that are presented in Table 2 also suggested that the tree-ring white noise residual series was a reliable estimator of the temperature series (Fritts, 1976). Given the high quality of these results and a desire to consider the fullest possible range of

Table 2. Calibration and verification test summary. (Symbols explained below)

Calibration period		Verification period						
	r^2_a		r^2	s	P	t	W	RE
1926-1969	.42a	1882-1925	.75a	a	a	a	a	.60
1882-1925	.75a	1926-1969	.42a	a	a	a	a	.18
1912-1969	.58a	1883-1911	.56a	a	a	a	a	.61
1883-1911, 1941-1969	.54a	1912-1940	.66a	a	a	a	a	.67
1883-1940	.62a	1941-1969	.51a	a	a	a	a	.52
1904-1969	.59a	1882-1903	.54a	a	a	r	a	.64
1882-1903, 1926-1969	.48a	1904-1925	.86a	a	a	r	a	.77
1882-1925, 1948-1969	.65a	1926-1947	.45a	a	a	a	a	.15
1882-1947	.66a	1948-1969	.36a	r	r	a	a	.40
FINAL CALIBRATION 1881-1969 $r^2 = .60$								

$r_a^2 = r^2$ adjusted for degrees of freedom, alpha = .01
 r^2 = variance explained, alpha = .01
s = first difference sign test, alpha = .01
P = product means test, alpha = .01
t = Student t-test, alpha = .10
W = Wilcoxon matched pairs signed ranks test, alpha = .10
RE = reduction of error test
a = null hypothesis not rejected
r = null hypothesis rejected

covariation in developing the final calibration equation used for reconstruction, data for the full 89 years of common period were analyzed. Sixty percent of the variance in the two series is

in common, the covariance is significant at the 0.001 level and the regression residuals do not show abnormal outliers or significant autocorrelation. A reconstruction of average June-July

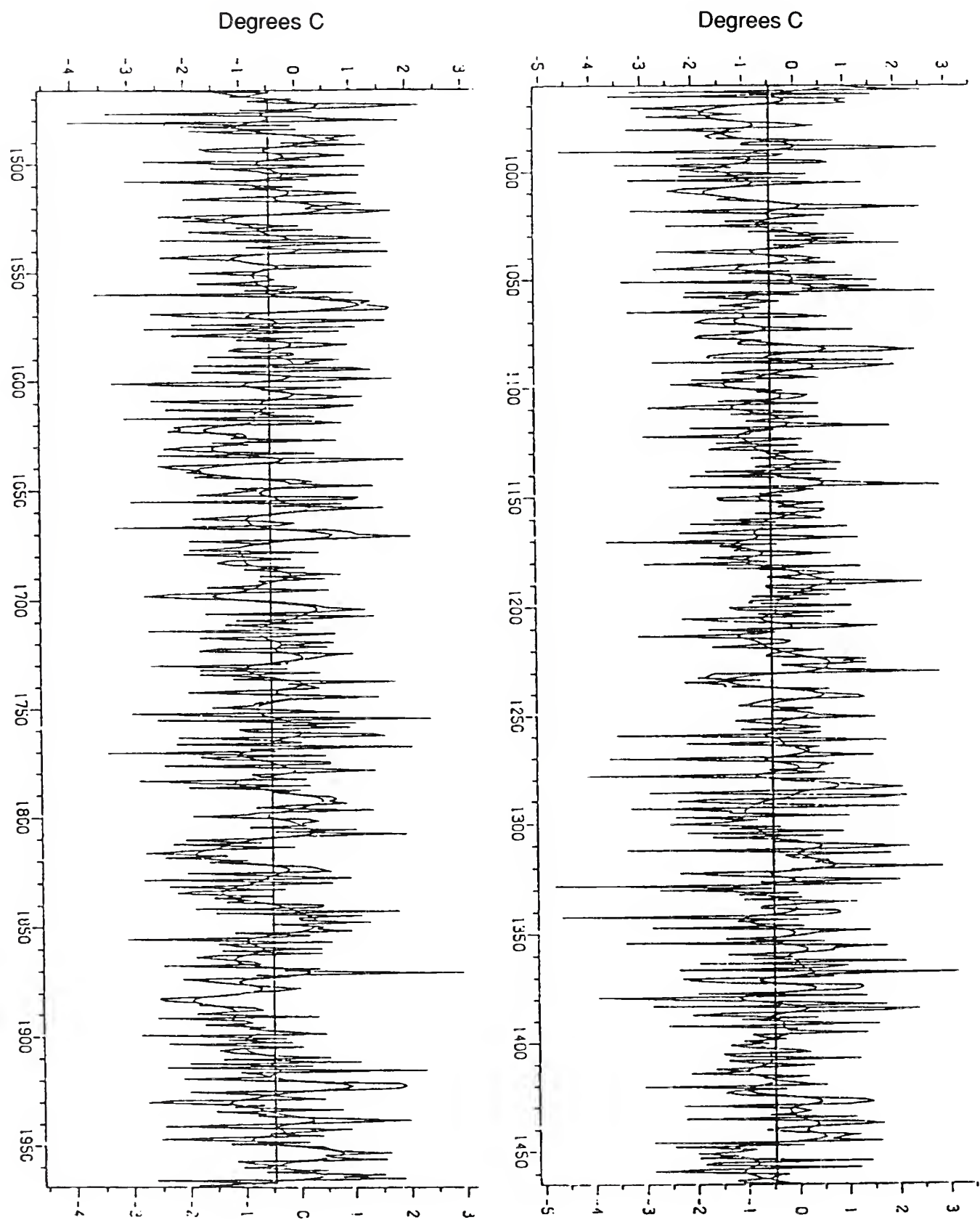


Figure 1. Reconstructed mean June-July temperature departures, North Polar Urals, A.D. 961-1969

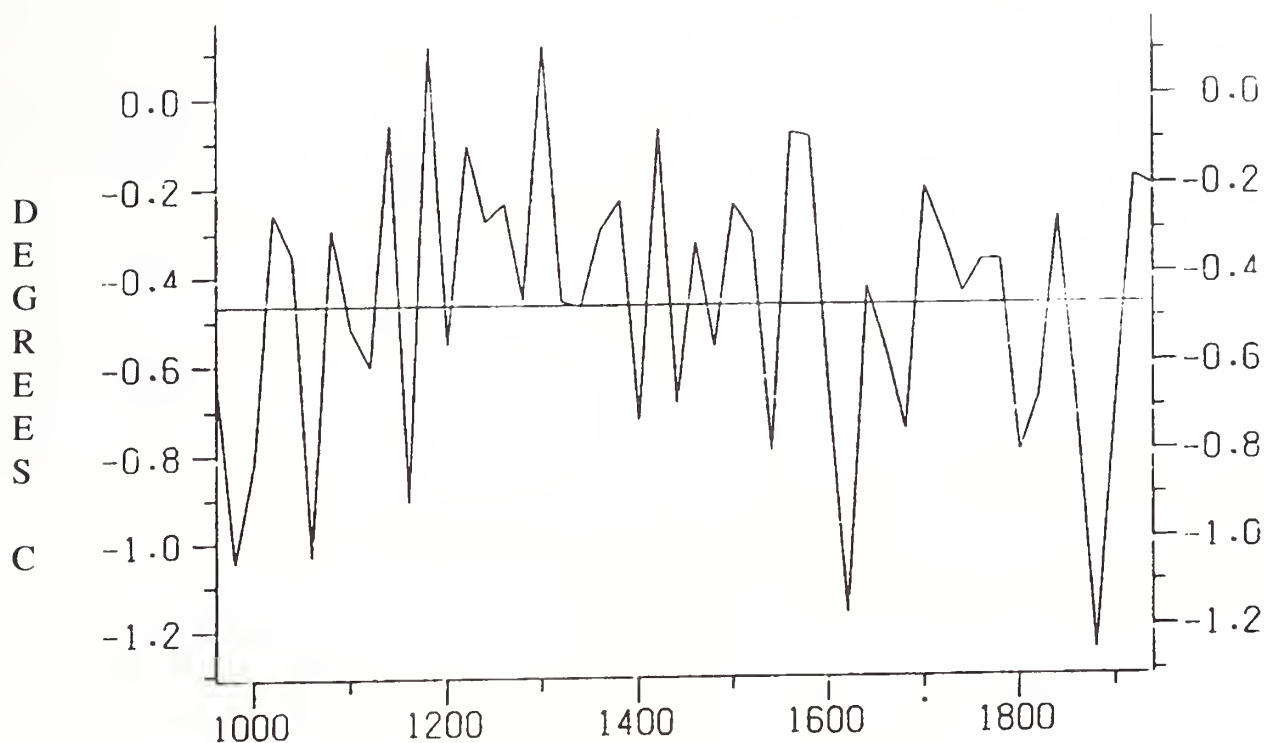


Figure 2. Twenty year averages of reconstructed mean June-July temperature departures, North Polar Urals, A.D. 961-1969.

temperature departures was then developed for the period of A.D. 961-1969.

Reconstructed early summer temperature deviations over the past millennium are illustrated in Figure 1. Twenty year non-overlapping averages of those values are shown in Figure 2 to aid in recognition of predominant kinds of trends. One of the more striking patterns is the rise in values from near 1100 to the highs of the 1200's-1300's, followed on the long term by an overall decline in values, but with some increase since the lows of the 1600's. This larger pattern as well as several of the major peaks in values (near 1200, 1300, the mid-1500's and near 1700) are reminiscent of Lamb's (1966) reconstructed temperature record for central England. Additionally, certain major features of our reconstruction such as the low values of the 1600's, and those of the 1800's that are followed by a sharp increase in 20th century values are seen in many other high latitude and altitude tree-ring chronologies. Space limitations here preclude further discussion of this.

Now, most of the constituent tree-ring

series forming the chronology range in age from about 220-400 years, although a few are of shorter length. Given this, and the fact that standardization can remove trends that are at the same or greater length than the series in question, the ability of this reconstruction to mirror longer term trends may be questioned. There are, however, important field observations that bear on this issue. Dead series in this chronology are from elevations of 100-120m above the highest currently living trees. All of the former that were living in the early mid-1600's had dramatic growth decline at that time and their demise occurred then or shortly thereafter. This is also the time period when the majority of the oldest living trees found at the current elevational treeline germinated, although some found here date to the mid-1500's. Therefore, it is possible that the longer term trends in temperature departures are at least reasonably estimated. The two different elevational groupings of trees provided continuous monitors of temperature variation at their respective locations and sequentially their records may have captured those trends.

Further evaluation of the results obtained here may be possible as the development and analysis of other long tree-ring chronologies in the sub-Arctic proceeds (Bartholin, 1984). Quantitative information derived from a spatial field of long tree-ring chronologies should prove useful for evaluating models of long-term climatic variation on regional and hemispheric scales, or even for testing hypotheses about the global nature of phenomena such as the Little Ice Age (Grove, 1988).

Literature Cited

- Bartholin, T. S. 1984. Dendrochronology in Sweden. In *Climatic Changes on a Yearly to Millennial Basis*. N. A. Morner and W. Karlen (eds). Reidel Publishing Company.
- Briffa, K. R., P. D. Jones, J. R. Pilcher and M.K. Hughes. n.d. Reconstructing Summer Temperatures in Northern Fennoscandia Back to 1700 A.D. Using Tree-Ring Data from Scots Pine. In press, *Arctic and Alpine Research*.
- Box, G. E. P., and G. M. Jenkins. 1976. *Time Series Analysis: Forecasting and Control*. Holden-Day, San Francisco.
- Fritts, H. C. 1976. *Tree Rings and Climate*. Academic Press, London.
- Graybill, D. A. 1982. Chronology Development and Analysis. In *Climate from Tree Rings*. M. K. Hughes, P. M. Kelly, J. R. Pilcher, and V. C. LaMarche, Jr. (eds). pp. 21-28. Cambridge University Press, London.
- Graybill, D. A. 1985. *Western U. S. Tree Ring Index Chronology Data for Detection of Arboreal Response to Increasing Carbon Dioxide*. No. 026 in the U. S. Department of Energy Green Book Reports on the Response of Vegetation to Carbon Dioxide series. Laboratory of Tree-Ring Research, University of Arizona, Tucson.
- Grove, J. M. 1988. *The Little Ice Age*. Methuen.
- Jacoby, G. C. and E. R. Cook. 1981. Past Temperature Variations Inferred From a 400 Year Tree-Ring Chronology from Yukon Territory, Canada. *Arctic and Alpine Research* 13(4):409-418.
- Jones, P. D., S. C. B. Raper, B. D. Santer, B. S. G. Cherry, C. Goodess, R. S. Bradley, H. F. Diaz, P. M. Kelly and T. M. L. Wigley. 1985. *A Grid Point Surface Air Temperature Data Set for the Northern Hemisphere, 1851-1984*. U.S. DOE Technical Report, TR022, U. S. Department of Energy Carbon Dioxide Division, Washington D.C.
- Kelly, P. M., P. D. Jones, C. B. Sear, B. S. G. Cherry and R. K. Tavakol. 1982. Variations in Surface Air Temperatures: Part 2, Arctic Regions, 1881-1980. *Monthly Weather Review* 110:71-83.
- Lamb, H. H. 1966. *The Changing Climate*. Methuen.
- Shiyatov, S. G. 1986. *Dendrochronology of the Upper Forest Boundary in the Urals*. Nauka, Moscow (in Russian).
- Shiyatov, S. G. and V. S. Mazepa. 1987. Some New Approaches in the Construction of More Reliable Dendrochronological Series and in the Analysis of Cycle Components. *Methods of Dendrochronology-I, Proceedings of the Task Force Meeting on Methodology of Dendrochronology: East/West Approaches*. IIASA, Laxenberg, Austria.
- Wigley, T. M. L., K.R. Briffa and P. D. Jones. 1984. On the Average Value of Correlated Time Series with Applications in Dendroclimatology and Hydrometeorology. *Journal of Climate and Applied Meteorology* 23:201-213.
- Wonnacott, T. H. and R. J. Wonnacott. 1981. *Regression: A Second Course in Statistics*. Wiley. New York.

Dendrochronology and Spatial Analyses

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Abstract

The linear aggregate model (Cook, 1987) is proposed as a statistical tool to separate sources of variability inherent in tree-ring series. Use of multivariate spatial statistics is introduced as a technique to investigate the spatial covariation of atmospheric deposition and tree-ring indices.

Introduction

Tree ring data offers a unique historic record of past endogenous and exogenous influences on tree growth. It is this historical tracking that can be exploited to assess the possible impacts of atmospheric deposition on forests. To adequately address the atmospheric deposition impact hypothesis, it is necessary that other ecological and environmental variables that influence tree growth be accounted for. How to extract the signal of interest is not a simple concept. Signal is defined here as that information in the tree ring series which is relevant to the study of a particular problem (Cook, 1987). A tree ring series can be thought of as consisting of several to many unobserved signals. Some of these signals will be of no interest or cannot be accounted for, as such these sources or variation will be considered as noise. We thus wish to decompose the observed growth

rings into a number of signals which represent the environmental influences on tree growth.

Cook (1987) gives an excellent account of the likely sources of variation in tree ring series and provides a conceptual framework for the decomposition of growth rings in the form of a linear aggregate model. This model allows the identification of the likely signals influencing tree growth. Following Cook, a possible aggregate series can be expressed as:

$$R_t = A_t + C_t + \lambda D1_t + \lambda D2_t + E_t$$

where R_t is the observed ring-width series, A_t , the age-size related trend in ring-width, C_t , the climatic signal, $D1_t$, a pulse caused by a local (endogenous) disturbance, $D2_t$, a pulse caused by a standwide (exogenous) disturbance, λ , either 1 or 0 indicating presence or absence of a disturbance, and E_t , unexplained year-to-year variability.

A_t is the growth trend of the tree and, therefore, is a nonstationary process. The type of trend model chosen largely depends upon the situation. For open grown trees, a negative exponential curve can portray the expected growth trend. However, for trees strongly influenced by competition and disturbances in the forest, more flexible models are needed. For further insight, refer to Cook (1987).

C_t is the climatically related environmental variable. Precipitation, temperature, and the Palmer Drought Severity Index (Palmer, 1965) which are computed from average monthly temperature and precipitation data, are variables that can be obtained from the Historical Climatology Network (HCN) produced by NOAA (Boden, 1987). C_t is a common signal to all trees in a stand. The modeling methods of C_t are beyond the scope of this paper, but the following references are some suggested readings: Fritts *et al.*, 1971; Fritts, 1976; Guiot, 1985; Cook, 1988; Van Deusen, 1988.

$\lambda D1_t$ is a pulse that represents endogenous disturbance on a given tree. Such disturbances are common where stand development creates opportunities for release of trees that are in a state of suppression. This is commonly referred to as a gap-phase dynamic (White, 1979). An endogenous disturbance for a given tree will be considered a random event which is uncorrelated with endogenous disturbances in other trees. Thus, $\lambda=1$ or 0, depending on whether a disturbance has taken place or not.

$\lambda D2_t$ is the variable representing a stand-wide (exogenous) disturbance effect on tree growth. Insect and disease epidemics, fire, wind storms, forest management practices, and natural and anthropogenic deposition of chemicals are possibilities. Because $\lambda D2_t$ operates on a standwide basis, it should be present in all trees, quite unlike $\lambda D1_t$ which operates as a largely random pulse among trees. λ is either 1 or 0, depending on whether an exogenous disturbance has occurred or not.

E_t is the error term and represents the sources of variation not accounted for by the other model terms. It is assumed that the error term is uncorrelated in time and space between trees in the stand.

Standardization

There are a variety of standardization

techniques available. It is beyond the scope of this paper to thoroughly discuss the implications of alternative standardization techniques. The following, however, are excellent places to start: Fritts *et al.*, 1969, 1976; Warren, 1980; Cook, 1985; Monserud, 1986; Shiyatov and Mazepa, 1987; Van Deusen, 1987.

The essence of standardization is the estimation and removal of growth trend (A_t) from the ring-width series. Once this is accomplished, the original nonstationary ring widths are transformed into relative tree-ring indices that have a mean of 1.0 and constant variance. The relative index is computed by dividing each original ring width by its expected growth trend value, which is estimated by A_t ($I_t = R_t / A_t$). The expected value of I_t is 1.0. Clearly how close the growth trend mimics the ring widths determines the degree of homogeneity of variance about I_t . Care should be taken that the possible pollution signal is not removed by using a growth trend function that is much too flexible (Cook, 1985).

After standardization, a mean-value function can be computed based on averaging the index series for all trees in a given stand. At this point, the estimation of the climatic signal can begin. Past studies (Fritts, 1976) have generally used the arithmetic mean. I advocate the use of a robust mean. Cook (1987) indicates that the use of the biweight mean (Mosteller and Tukey, 1977) is a reasonable choice. The robust mean will discount the influence of outliers and thus reduce the variance and bias. Endogenous effects will cause outliers to appear in the index series, and can confound the estimation of the climate signal. The robust mean is one way to deal with these random pulses (outliers) and enable cleaner estimation of the climatic signal.

In the context of finding an air pollution signal, the purpose of estimating the climatic signal is to predict values of tree indices based on a climate model. This can then be used to test for nonclimatic influences on growth, for

example, pollutant deposition.

Autoregressive Disturbances

It is generally known that a certain amount of physiological preconditioning is present in tree-ring widths. This means that present growth is autocorrelated with past tree growth. These autocorrelated structures can be addressed by use of statistical models that account for this process. The general autoregressive (AR) process has the form (Box and Jenkins, 1970):

$$Z_t = e_t + \sum_{i=1}^p b_i Z_{t-i}$$

where, Z_t is the observed process for year t , e_t is a random shock that is not autocorrelated, and b_i are autoregressive coefficients of the AR(p) process. Past work by Cook (1985), and Monserud (1986) indicate that the best AR models generally fall in the AR(1)-AR(3) classes.

The consequence of autocorrelation is that the effect will be to degrade the signal to noise ratio. Thus, before estimating the climatic model, it is best to remove this component. The indices can be modelled and prewhitened as explained above.

Pollution Signal

Assume an enlightened estimation of the linear aggregate model (1). Suppose, however, a modification is made such that λD_2 is not estimated, but, instead, is now part of E_t , that is, $R_t = A_t + C_t + \lambda D_1 + E_t$. If E_t does, in fact, contain an exogenous disturbance effect that is spatially correlated on a large scale, hypotheses can be constructed to test for spatial correlation with a gradient in pollutant deposition. If the impact of pollution on radial growth is sufficiently strong, it should be possible to detect the signal after accounting for the influence of climate through the estimation of C_t . It is necessary that there is enough spatial coverage in 2-d (latitude and longitude) or 3-d (plus elevation) space, such that a range of ambient depo-

sition rates and tree-ring indices are available to develop a spatial response model between the pollution signal within E_t and the spatially correlated deposition variable.

Spatial Analysis

First, it must be demonstrated that enough pollutant deposition information exists in time and space to produce a reliable spatial model in at least 2-d space over a period of years. This time-space replication is necessary so that a clear picture of areas with high, moderate and low levels of deposition become evident. Secondly, there must also be enough geographic coverage of tree-ring chronologies. Given this, the problem of how to model spatial variation can proceed.

The use of regionalized variables (geostatistics) is a reasonable first step to investigate spatial variation and covariation. Those unfamiliar with regionalized variables can reference Journel and Huijbregts (1978). Geostatistical theory is based on the observation that the variabilities of all regionalized variables have a particular structure. For this particular problem, the interest is in quantifying the spatial correlation that exists for a particular pollutant. That can be accomplished as follows: Consider observations of a pollutant of interest, and refer to these observations as z_i . The relation between pairs of points h intervals apart (distance of h between adjacent monitoring stations), can be expressed as the differences between all such pairs. The per-observation variance between pairs (Yates, 1948) is half this value: $\gamma(h) = 1/2 \text{ var}[z_i - z_{i+h}]$, where $\gamma(h)$ is known as the semivariance, and is a measure of the similarity, on average, between points a given distance, h , apart. The more alike the points, the smaller $\gamma(h)$ is.

The semivariance has characteristics which reveal the nature of the geographic variation in the variable of interest. In most instances, $\gamma(h)$ increases with increasing h to a maximum,

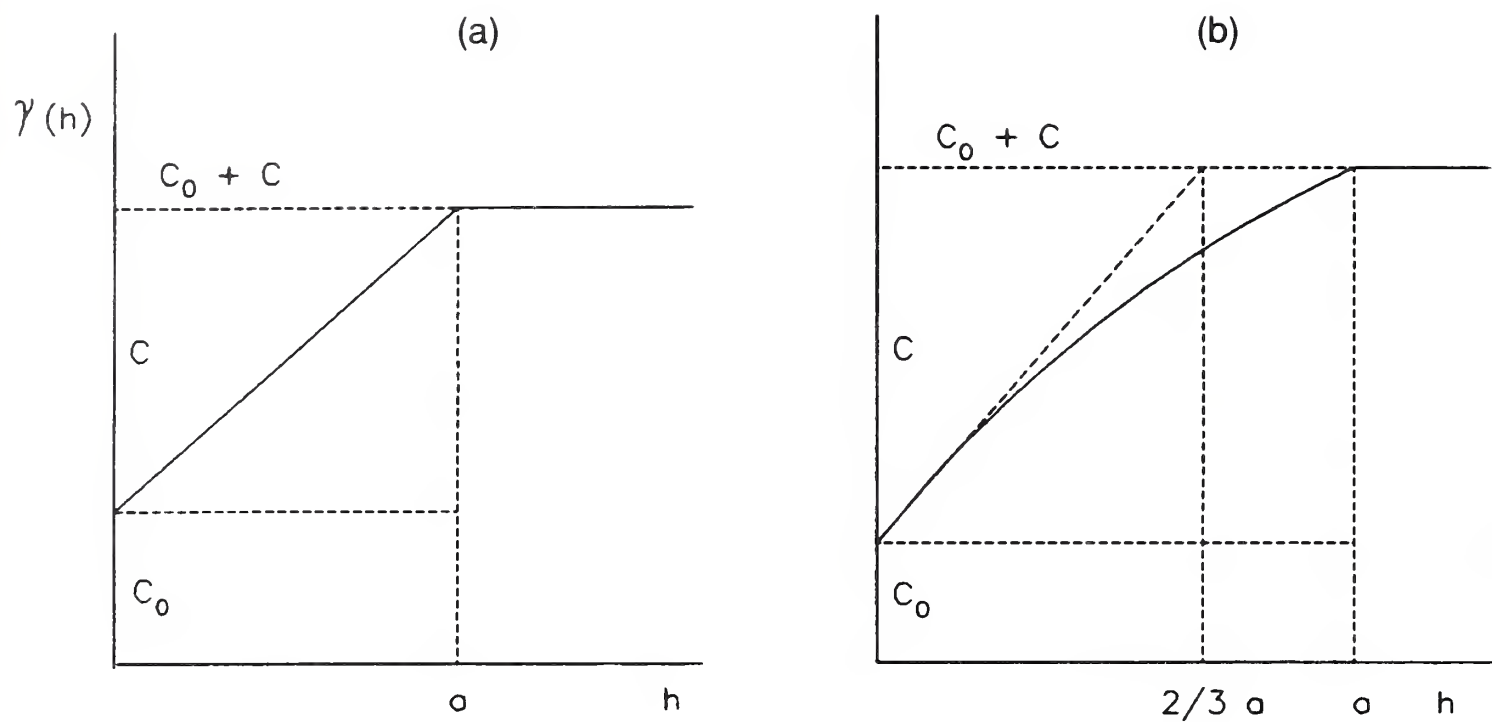


Figure 1. Theoretical semivariograms for (a) a linear model and (b) spherical model, illustrating the range, a , the sill c_0+c , and the nugget variance c_0 . The tangent to the curve at $h=0$ in (b) meets the horizontal for the total variance at $2/3 a$.

which is approximately the variance of the data. This maximum usually will occur at a moderate value of h , say “ a ” (Figure 1). The distance “ a ” is known as the range. If $\gamma(h)$ approaches the maximum asymptotically then “ a ” may be chosen where $\gamma(h)$ becomes sufficiently close to the total variance. Points closer together than the range are spatially dependent; points further away have no relation to one another, unless periodic variation exists.

By definition, $\gamma(h)=0$ when $h=0$. However, any smooth function that approximates the semivariance is unlikely to pass through the origin. Instead, a positive finite value for $\gamma(h)$ is present as h approaches 0. This intercept is the nugget variance, “ c_0 ” and is a measure of fluctuations over distances shorter than the sampling interval, and limits the precision of prediction.

The value at which $\gamma(h)$ levels out is known as the sill. It consists of the nugget variance plus a component “ c ” that represents the range of variance due to spatial dependence.

There is no general formula to describe the shape of semivariograms; a linear model $\gamma(h)=c_0 + mh$ is the simplest, and often can describe $\gamma(h)$ within the range, (i.e. $h=0$ to $h=a$). Various nonlinear models can be used, and a spherical model proposed by Matheron (1963) is often applicable:

$$\gamma(h) = c_0 + c\{3/2(h/a) - 1/2(h/a)^3\} \text{ for } 0 < h < a$$
$$\gamma(h) = c_0 + c \text{ for } h > a$$

With the background information above, an investigation into the possible spatial covariation of tree-ring indices and pollutant deposition can proceed.

An Example

Monitoring of atmospheric deposition in Pennsylvania indicates that precipitation here can be characterized as a dilute aqueous solution of sulfuric and nitric acids. This precipitation generally produces a west (high deposition) to east (low deposition) gradient of H^+ across the state (Lynch and Corbett, 1983). The pattern of SO_4 deposition is less distinct, but evident. Air quality monitoring has shown a similar

deposition pattern from 1982-85. This indicates that the same areas have perennially received higher deposition rates than others; thus, if necessary, we can likely collapse over years as long as local emission sources and long-range transport are relatively stable.

Presently, there are 16 atmospheric monitoring stations in Pennsylvania where data are available. Additional NADP sites are available from surrounding states. Precipitation amount (cm), concentrations (mg/l) of H^+ , SO_4 , NO_3 and annual deposition (g/m²) of the same ions are measured at each station. Tree-ring data are available at 200 forest survey plots that meet the criteria of 1) having two prior measurement occasions, 2) being free from disturbance throughout their history, and 3) being classified as either oak-hickory or northern hardwoods forest types. The forest plots were systematically selected to assure good spatial distribution for the western and central portions of the state.

The covariance analysis of the atmospheric deposition and concentration data with the tree-ring data should investigate both spatial and intervariable correlation. This can be done through co-kriging where the data from one or more auxiliary variables (i.e. deposition or concentration of pollutants) is used to estimate the response variable (i.e. tree-ring index).

Suppose now that an analysis to investigate the spatial covariation of tree-ring indices and SO_4 is proposed. Specifically, the term E_t from the linear aggregate model that hopefully contains an exogenous pollution signal will be correlated with SO_4 . The test of spatial covariation is provided by computing the cross semivariogram. The cross semivariogram can be estimated by:

$$\gamma_{12}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z_1(x_i) - z_1(x_i + h)] [z_2(x_i) - z_2(x_i + h)]$$

where $N(h)$ is the number of pairs of values $\{[z_1(x_i), z_1(x_i+h)], [z_2(x_i), z_2(x_i+h)]\}$ separated by a distance h .

Estimation of a particular variable for an unsampled location is done as follows. Consider an estimate of variable z_2 is needed. This can be done by using the co-kriging equation,

$$Z_2(x_0) = \sum_{i=1}^{N_1} \lambda_{1i} Z_1(x_{1i}) + \sum_{j=1}^{N_2} \lambda_{2j} Z_2(x_{2j})$$

where, λ_{1i} and λ_{2j} are the weights associated with Z_1 and Z_2 , and N_1 and N_2 are the number of neighbors of Z_1 and Z_2 involved in the estimation of the unsampled location x_0 . As the actual mathematics are beyond the scope of this paper, those unfamiliar with co-kriging and cross semivariogram estimation are directed to the following references (Vauclin *et al.*, 1983; Journel and Huijbregts, 1978).

An extension to other pollutant variables can proceed as above, and there is also the possibility of combining multivariate techniques with co-kriging.

Literature Cited

- Boden, T.A. 1987. *United States historical climatology network (HCN) serial temperature and precipitation data*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Box, G.E.P. and G. Jenkins. 1970. *Time series analyses: forecasting and control*. San Francisco. Holden-Day. 553 pp.
- Cook, E.R. 1985. *A time series approach to tree-ring standardization*. Ph.D. dissertation. The University of Arizona, Tucson.
- Cook, E.R. 1985. The use and limitations of dendrochronology in studying effects of air pollution on forests. In *Proceedings of NATO Advanced Research Workshop: Effects of Acidic Deposition on Forests, Wetlands, and Agricultural Ecosystems*. Toronto, Canada.

- Cook, E.R. 1987. The decomposition of tree-ring series for environmental studies. *Tree-Ring Bulletin* 47:37-59.
- Cook, E.R. 1988. A tree-ring analysis of red spruce in the southern Appalachian mountains. P.C. Van Deusen, (ed). *In Analyses of Great Smoky Mountain Red Spruce Tree Ring Data*. Gen. Tech. Rep. 50-69. New Orleans, LA:USDA-FS, Southern For. Exp. Sta. 67 p.
- Fritts, H.C., J.E. Mosimann, and C.P. Bottorff. 1969. A revised computer program for standardizing tree-ring series. *Tree-Ring Bulletin* 29:15-20.
- Fritts, H.C., T.J. Blasing, B.P. Hayden, and J.E. Kutzbach. 1971. Multivariate techniques for specifying tree growth and climate relationships and for reconstructing anomalies in paleoclimate. *Journal of Applied Meteorology* 10:845-864.
- Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press. London.
- Guiot, J. 1985. The extrapolation of recent climatological series with spectral canonical regression. *Journal of Climatology* 5:325-335.
- Journel, A.G., and Ch. J. Huijbregts. 1978. *Mining Geostatistics*. Academic Press. New York.
- Lynch, J.A., and E.S. Corbett. 1983. *Atmospheric deposition: spatial and temporal variations in Pennsylvania* 1982. Instit. for Res. on Land and Water Resour. LW8313. Penn. St. Univ., University Park. 73pp.
- Matheron, G. 1963. Principals of Geostatistics. *Economic Geology*. 58: 1246-1266.
- Monserud, R.A. 1986. Time series analyses of tree-ring chronologies. *Forest Science* 32:349-372.
- Mosteller, F., and J.W. Tukey. 1977. *Data Analysis and Regression*. Addison-Wesley, Reading, Massachusetts.
- Palmer, W.C. 1965. *Meteorological drought*. Weather Bureau Research Paper Number 45. U.S. Department of Commerce, Washington, DC. 58 p.
- Shiyatov, S.G., and V.S. Mazepa. 1987. Some new approaches in the consideration of more reliable dendroclimatological series and in the analysis of cycle components. L. Kairiukstis, Z. Bednarz, and E. Feliksik (eds.). *In Proceedings of: Methods of Dendrochronology- 1*. International Institute for Applied Systems Analysis/Polish Academy of Science-Systems Research Institute. Warsaw, Poland, pp. 87-96.
- Vauclin, M., S.R. Vieira, G. Vachaud, and D.R. Nielsen. 1983. The use of co-kriging with limited field soil observations. *Soil Sci. Soc. Am. J.* 47:175-184.
- Van Deusen, P.C. 1987. Testing for stand dynamics effects on red spruce growth trends. *Canadian Journal of Forest Research* 17:1487-1495.
- Van Deusen, P.C. 1988. Red spruce tree ring analysis using a Kalman filter. P.C. Van Deusen, (ed). *In Analyses of Great Smoky Mountain Red Spruce Tree Ring Data*. Gen. Tech. Rep. 50-69. New Orleans, LA: USDA-FS, Southern For. Exp. Sta. 67 p.
- Warren, W.G. 1980. On removing the growth trend from dendrochronological data. *Tree-Ring Bulletin* 40:35-44.
- White, P.S. 1979. Pattern, process and natural disturbance in vegetation. *Botanical Review* 45:229-299.
- Yates, F. 1948. Systematic sampling. *Physiological Transactions of the Royal Society*. London, Ser. A 241:345-377.

100-Year Records of Forest Productivity at High Elevations in Western Washington, USA

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Introduction

Recent variations in forest productivity are a major interest in North America and Europe as concern grows over reports of forest declines due to acid rain and atmospheric deposition (Johnson and Siccama, 1983, 1984; Krause *et al.*, 1983; Morrison, 1984; Prinz *et al.*, 1983). The accurate assessment of production losses from these factors requires a knowledge of the productivity of forest stands in the absence of air pollution and the natural variability of production over time. Unfortunately, estimates of forest production require intensive research projects (Grier and Logan, 1977; Sprugel, 1984; Cooper, 1981) and, as a consequence, the productivity of many forest types in these regions are not well known.

Net primary productivity (annual production of biomass per unit area) has been studied more intensely in conifer forests than in any other forest type (Sprugel, 1985). Empirical studies of several different species in different climatic and geologic settings have documented

productivity changes following major stand disturbances (Grier and Logan, 1977; Tadaki *et al.*, 1977; Yarie and Van Cleve, 1983; Sprugel, 1984). Although the absolute rates of change differ among forest types depending on the lifespans of the species involved, all studies show generally similar trends during stand development and aging. These trends are summarized below as described by Sprugel (1985).

Annual productivity decreases immediately after disturbance, but increases rapidly as new trees become established on the site. The largest component of production during early stages of stand development comes from the production of leaf biomass. Following crown closure, leaf production stabilizes and the relative contribution of woody tissue increases. Total stand productivity stabilizes in mature stands, but generally decreases as stands reach old age. Production declines in old stands are presumably due to increased stand respiration related to the increasing biomass of woody tissue, or to a decrease in nutrient availability.

The objective of our study was to assess the natural variability of net primary production of old-growth conifer stands on upper slopes of the Cascade Mountains, Washington. We were particularly interested in the effect of annual variations in climate on the forest production, as prior work (Grier and Running, 1977; Gholz, 1979) suggests that these forests should be susceptible to annual variations in temperature. Our study also provides baseline information for assessing present and future pollution effects in these mountains.

Study Area

Geology

The Cascade Range, WA, is a north-south trending mountain chain with maximum elevations typically reaching 2000 to 3000 m. Several volcanic cones rise more than 1000 m above the major peaks of these mountains (Highsmith, 1973). This range was covered by extensive alpine glaciers during the most recent glaciation (Porter, 1984). Soils are generally thin and developed in glacial till capped by numerous tephra layers originating from nearby volcanoes (Franklin and Dyrness, 1973).

Climate

Westerly air from the Pacific Ocean dominates the western slopes of the Cascades during all seasons of the year (Highsmith, 1973). Orographic lifting of moist air results in high precipitation in the mountains, particularly as snow in the winter. Annual snowfall is commonly more than 1500 cm at upper elevations (1500-2000 m) in these mountains. Snow often remains on the ground at upper elevations until early July. Precipitation is strongly seasonal, however, with only 20 percent of the average annual precipitation occurring during the growing season.

The proximity of the Pacific Ocean has a mitigating effect on seasonal temperature fluctuations in the western Cascades.

At upper elevations in these mountains, minimum January temperatures are approximately -10 to -15°C and average maximum July temperatures are generally $+15^{\circ}\text{C}$.

A recent dendroclimatic reconstruction for the west Cascade Mountains shows a 1°C increase in mean annual temperature between the mid-19th and 20th centuries (Graumlich and Brubaker, 1986). This warming trend has caused a rapid recession of alpine glaciers (Burbank, 1981) and recent increase in tree establishment at treeline (Franklin *et al.*, 1971) in these mountains.

Forests

Three major forest zones (Franklin and Dyrness, 1973) cover the western slopes of the Cascade Mountains. The *Tsuga heterophylla* zone extends from lowland areas to approximately 700 m. Old-growth forests in this zone are dominated by *Pseudotsuga menziesii* (Douglas-fir) and/or *Tsuga heterophylla* (western hemlock), with lesser importance of *Thuja plicata* (western red cedar). These species are generally long-lived (600-1000 years) and reach massive sizes (3 m in diameter, 100 m in height). Stands within this zone have shown some of the highest biomass and annual production rates recorded for coniferous forests in the world (Lassoie *et al.*, 1985).

The *Abies amabilis* zone, extending from approximately 700 to 1500 meters, is dominated almost exclusively by *Abies amabilis* (Pacific silver fir). Trees in this zone are smaller than those of the *Tsuga heterophylla* zone and net primary productivity is generally two-thirds that of the *Tsuga heterophylla* zone (Lassoie *et al.*, 1985). The lower productivity of *Abies amabilis* forests is thought to result from the detrimental effects of shorter and cooler growing seasons on rates of net photosynthesis and nutrient release by decomposition and mineralization at high elevations (Lassoie *et al.*, 1985).

The *Tsuga mertensiana* zone (1000 to 1500 m) is the highest forest zone of the western Cascade Mountains. These forests are dominated by *Tsuga mertensiana* (mountain hemlock) with varying proportions of *Abies amabilis*, *Chamaecyparis nootkatensis* (Alaska yellow cedar) and *Abies lasiocarpa* (subalpine fir). Old trees (600-1000 yrs) are relatively common; however, tree sizes are generally small compared to those of lower forest zones. The productivity of these forests has not been previously studied, but is considered to be less than that of lower forest zones.

Methods

Field Sampling

The following criteria were used to select plots for sampling: 1) tree ages of at least 300 years, 2) no evidence of tree mortality within the plot and within 10 meters of the plot perimeter, and 3) no evidence of unusual crown damage to trees within the plot. In each plot, increment cores were collected at 1.4 m height from all trees greater than 15 cm in diameter. The diameters of all sample trees were measured at 1.4 m height. The locations of the plots analyzed in this study are shown in Figure 1.

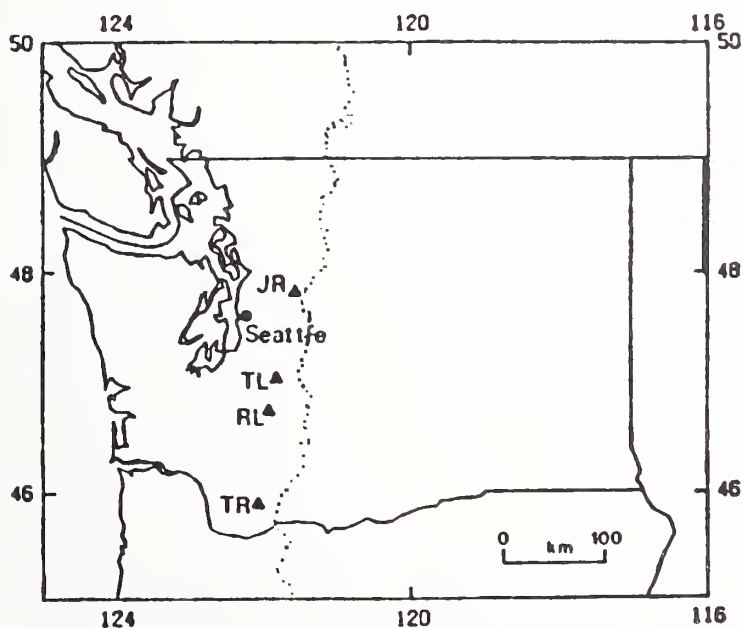


Figure 1: Locations of sites analyzed for net primary production and the Seattle climatic station. The dashed line represents the crest of the Cascade Mountain Range.

Laboratory analysis

All cores were mounted in permanent holders, sanded to a high polish and cross-dated with other cores from the plot and with existing tree-ring chronologies from the west Cascade Mountains (Brubaker, 1980; Graumlich and Brubaker, 1986). Annual ring widths were measured to the nearest 0.01 mm using a Bannister incremental measuring machine.

Estimation of Net Primary Production

Net primary production (NPP) is defined as the excess of annual gross photosynthesis over respiration (Odum, 1969). In practice, gross photosynthesis and respiration are difficult to measure in field situations and few studies have attempted to quantify these processes in forest stands (Assman, 1970; Sprugel, 1984). More commonly, NPP is estimated by the equation (Grier and Logan, 1977; Fujimori *et al.*, 1976):

$$NPP = B + D + G$$

where,

B = annual increment of living biomass of trees, shrubs and herbaceous plants

D = annual loss of living biomass of trees, shrubs and herbaceous plants due to natural mortality

G = annual loss of living biomass of trees, shrubs and herbaceous plants due to grazing.

Several simplifying assumptions enabled us to use this equation to reconstruct NPP back in time. Biomass losses to grazing were considered negligible because insect defoliation and grazing by mammals are unimportant in mature stands of western Cascade forests (Grier and Logan, 1977). Similarly, the contribution of understory species and small trees (<15 cm diameter at 1.4 meters) to total primary production of old stands is negligible (Grier and Logan, 1977). Estimating NPP was thus reduced to determining the biomass increment and mortality of large trees.

The major difficulty in assessing NPP by this equation is in determining the dates of tree mortality and sizes of such trees at the time of their death. In order to avoid the uncertainties of characterizing tree mortality, we selected plots free of signs of mortality (downed logs and raised linear surfaces). The death of trees less than 15-20 cm in diameter may have gone undetected, but trees of this size are unimportant in production budgets of old-growth forest stands (Grier and Logan, 1977).

We were thus able to estimate past NPP solely by determining the past biomass increments of trees alive at the time of sampling. Biomass increments were calculated by subtracting the estimates of total tree biomass of the plots between successive years. The components of tree biomass (foliage, stem wood, stem bark, and living and dead branches) for each year were calculated from standard regression equations (Gholz *et al.*, 1979) relating stem diameters to tree biomass components. These equations are of the form:

$$\ln Y = a + b \ln X$$

where,
Y = biomass of foliage, stem wood, stem bark, or branches
X = stem diameter
a, b = regression coefficients

We used species-specific regression coefficients established in previous studies (Gholz *et al.*, 1979), which had destructively sampled trees of each species and compared tree diameters to weights of tree biomass components. The total plot biomass for each year was calculated by summing the biomass components across all trees in the plot, as calculated from the diameters of trees in that year.

Comparisons of Productivity and Climate

The variations in NPP at the four sites were summarized by principal components analysis. Factor scores of the first principal component, representing the most important common variation in NPP among the series, were used as a record of variations in regional forest productivity for comparisons with climatic

Table1. Characteristics of sample plots.

Forest Zone	<i>Tsuga heterophylla</i>	<i>Abies amabilis</i>	<i>Tsuga mertensiana</i>	
Site	TR	TL	RL	JR
Latitude	45°52'	47°45'	47°02'	46°45'
Longitude	122°05'	121°15'	121°50'	121°56'
Elevation (m)	1200	1400	1440	1460
Plot size (ha)	0.032	0.046	0.051	0.026
No. Trees	27	20	14	24
Oldest Trees (yrs)	630	510	370	560
Percent of total biomass by species (1979) data:				
<i>T. heterophylla</i>	100	—	—	—
<i>A. amabilis</i>	—	52	27	4
<i>T. mertensiana</i>	—	48	69	96
<i>Chamaecyparis nootkatensis</i>	—	—	4	—

data. These scores were compared to climatic data from Seattle, WA (47° 39', 122° 18') using simple correlation and cross-spectral analyses. Seattle is the closest station to the sampling sites having a long meteorological record (1983-1980). Climatic data were summarized as average summer (June-September) temperatures and water year totals (the sum of precipitation from the preceding October through the September of the growth year).

Results

The sampled stands come from each of the three major forest zones of the west Cascade Mountains, WA (Table 1). Stand ages, as indicated by the age of the oldest tree, ranged from 370 to 630 years.

Current (1980) net primary production ranged from approximately 5 to 10 metric tons per hectare per year. The records NPP at all sites shows strikingly similar trends (Fig. 2): 1) increasing from 1880-1980, 2) decreasing or remaining stable from 1910 to 1935, 3) increasing from 1935 to 1960, and 4) remaining relatively stable from 1960 to 1980. The average increase in NPP at each sites between the first three decades (1880-1909) and last three decades (1950-1979) of

the record was 60 percent. Correlations of NPP among sites are positive and highly significant, ranging from .46 to .83. The first principal component explains 81 percent of the variation in the data and represents the positive correlation of NPP among all sites.

The time series of factor scores for the first component represents the common variation in

NPP at the four sites. In subsequent analyses, this series was considered to be a record of regional NPP, which represents diverse forest types in the west Cascade Mountains. The regional NPP record shows strong similarity to summer temperature trends ($r = .46$). The correlation of NPP with precipitation, although significant, is less strong ($r = .21$).

The purpose of the cross spectral analysis was to identify those temporal frequencies that most closely associate NPP with

temperature and precipitation. The squared coherency, analogous to the square of the correlation coefficient between two time series

calculated at different frequencies, revealed that NPP is associated with temperature over periods of 6 years and greater and with precipitation at periods of 3 years and less. In agree-

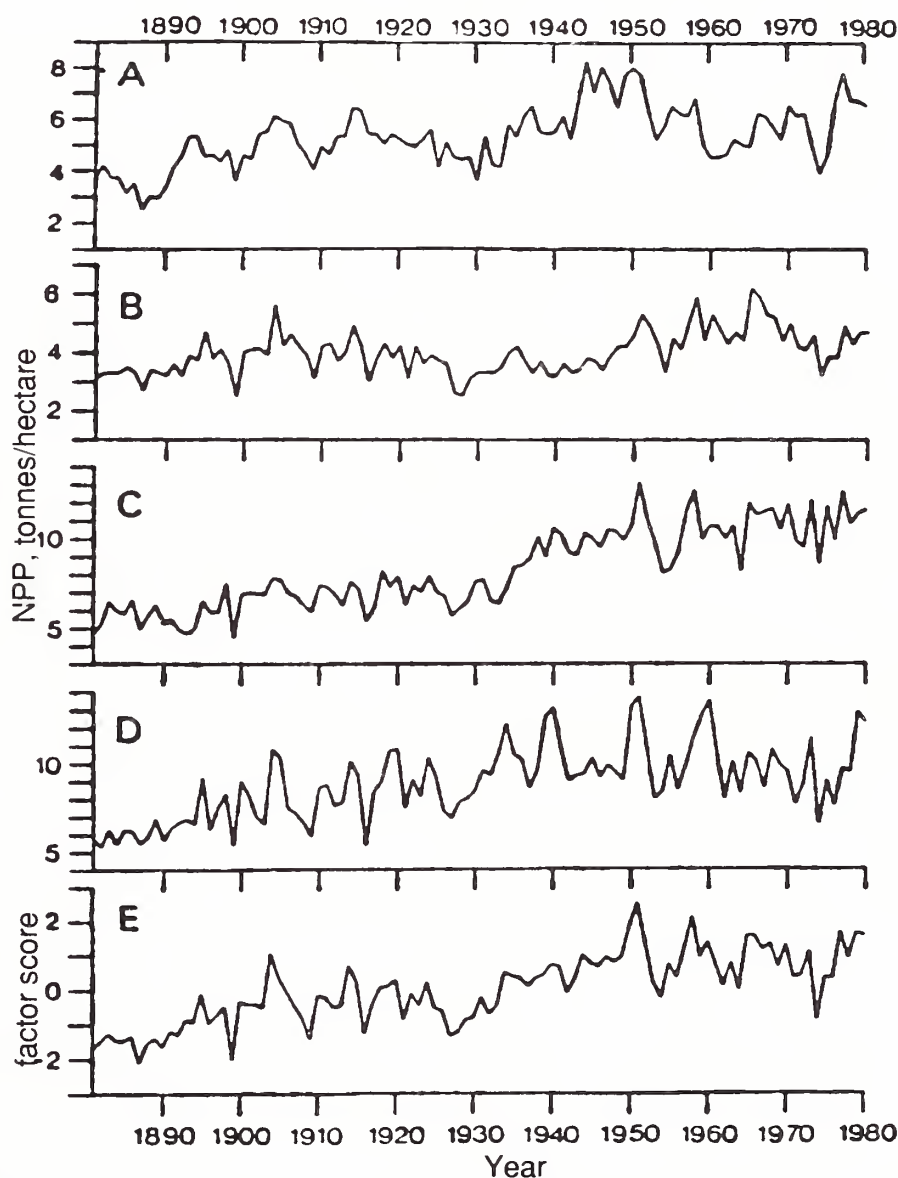


Figure 2. Annual estimates of NPP for forest stands on the upper slopes of the Cascade Range, Washington. (A-D) NPP estimates for four individual sites (see Table 1). (E) Factor scores obtained from the principal component analysis of the four series (A-D).

ment with the results of the correlation analyses, the association of NPP with temperature is much stronger than that of NPP with precipitation.

Discussion

The net primary productivity of stands sampled in this study are similar to values reported elsewhere in the west Cascades (Lassoie *et al.*, 1985). Thus, the current and, by implication, past productivity of our stands appears to be representative of forests in much of the western Cascade Mountains.

The similarity of NPP trends at the four sites is strong evidence that factors operating at a regional scale are important in determining the productivity of forests in these mountains. Although local disturbances and processes of stand dynamics may be important determinants of productivity in individual stands, these factors cannot explain the consistent productivity trends that we have observed in stands of different ages, species, and geographic locations. The significant statistical association of regional NPP records with temperature and precipitation records suggests that recent climatic variations, particularly variations in summer temperature, have been important factors controlling the productivity of western Cascade forests over the past century. Variations in global atmospheric

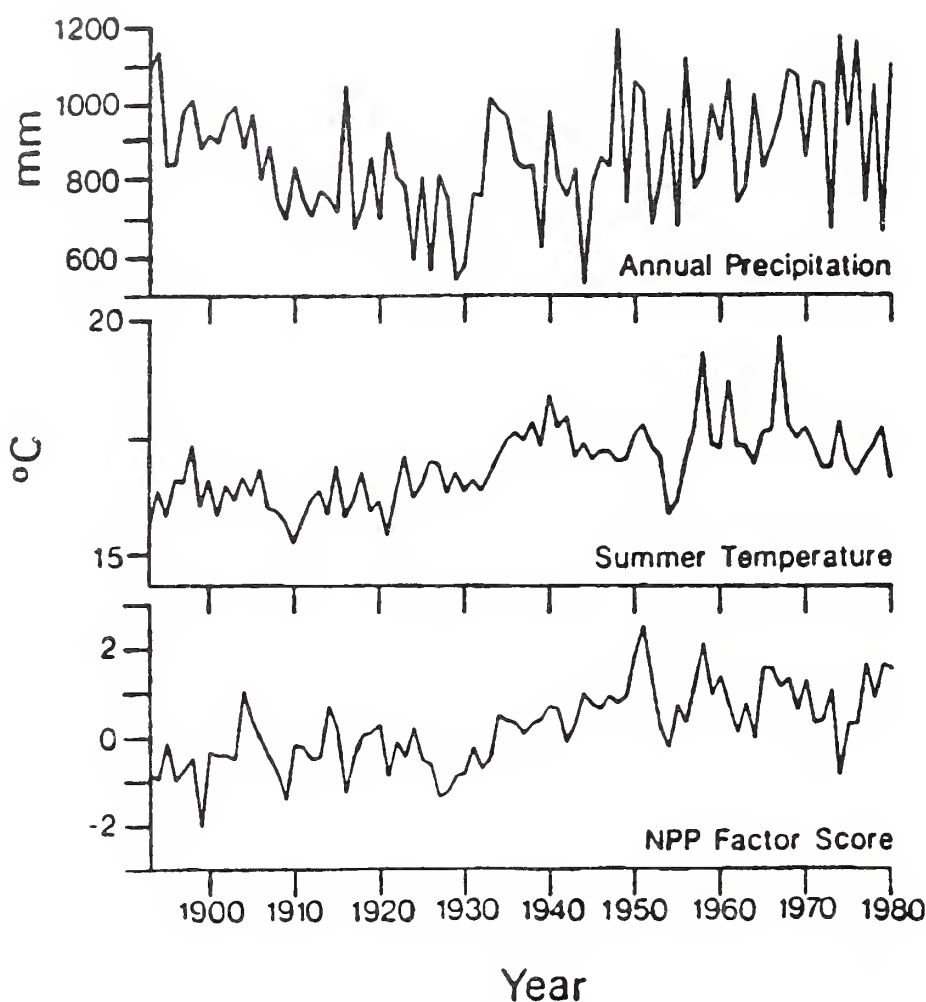


Figure 3. Annual precipitation and summer temperature, Seattle, Washington, (1893-1979) and time series of NPP factor scores, as in Figure 2 E.

carbon dioxide have apparently not directly affected forest productivity in this region (Graumlich *et al.*, in review). Likewise, no evidence exists for a production decline due to air pollution (Graumlich *et al.*, in review).

Temperature and precipitation can influence NPP through a variety of processes (Lassoie *et al.*, 1985). Precipitation variations predominantly affect short-term processes regu-

lating tree water balance, such as stomatal responses to xylem pressure potential and vapor pressure deficits. The effects of temperature are more complex, including short-term influences on photosynthesis, cell division, and water and nutrient uptake, as well as longer-term controls over leaf production, allocation of carbon to above- and below-ground parts, and rates of decomposition and mineralization. Differences in the way temperature and precipitation affect production-limiting processes may be responsible for the differences in the time scales over which NPP is correlated with these factors.

Our results also have implications for other studies of forest productivity in this region, and possibly in other regions where productivity responds strongly to temperature variations. Because the strongest relationship between

temperature and productivity is over long time periods (greater than 6 years), short-term measurements of temperature and productivity may not adequately specify the nature of the relationship between these variables. In addition, since NPP at each site varies substantially over short time periods, conventional practices of estimating NPP based on 1-to-5 year records of biomass increment may not accurately reflect long-term forest production rates.

Conclusions

The natural variability of productivity of upper elevation Cascade Mountain sites is great and controlled primarily by variations in summer temperature. NPP increased by 60 percent over the period 1880-1979. Thus, prior to 1980 these forests showed no evidence of a substantial decline in productivity that could be attributed to atmospheric pollution.

Literature Cited

- Assmann, E. 1970. *Principles of forest yield studies in the organic production, structure increment, and yield of forest stands*. Pergamon Press, Oxford, England.
- Brubaker, L. B. 1980. Spatial anomaly patterns of tree growth in the Pacific Northwest. *Ecology* 61:798-807.
- Burbank, D. W. 1981. A chronology of late Holocene glacier fluctuations at Mt. Rainier, Washington. *Arctic and Alpine Research* 13:369-386.
- Cooper, A. W. 1981. Above-ground biomass accumulation and net primary production during the first 70 years of succession in *Populus grandidentata* stands on poor sites in northern Lower Michigan. pp. 339-360, In West, D.C., H.H. Shugart and D.B. Botkin (eds.), *Forest Succession*. Springer-Verlag. New York, New York, USA.
- Franklin, J. F. and C. T. Dyrness. 1973. *Natural vegetation of Washington and Oregon*. United States Department of Agriculture Forest Service General Technical Report PNW-8.
- Franklin, J. F., W. H. Moir, G. W. Douglas, and C. Wierg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic and Alpine Research* 3:215-224.
- Fujimori, T., S. Kawanabe, H. Saito, C. C. Grier, and T. Shidei. 1976. Biomass and primary production in forests of three major vegetation zones of the northwestern United States. *Journal of the Japanese Forestry Society* 58:435-41.
- Gholz, H. L. 1979. *Limits on above-ground net primary production, leaf area, and biomass in vegetational zones of the Pacific Northwest*. PhD thesis, Oregon State University, Corvallis, Oregon.
- Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown. 1979. *Equations for estimating biomass and leaf area of plants in the Pacific Northwest*. Forest Research Laboratory, Oregon State University. Research paper 41. 37 pp.
- Graumlich, L. J. and L. B. Brubaker. 1986. Reconstruction of annual temperature (1590-1979) for Longmire, Washington, derived from tree rings. *Quaternary Research* 25:223-234.
- Graumlich, L. J., L. B. Brubaker, and C. C. Grier. Increasing net primary productivity in Washington forests during the last 100 years. Climatic Change. In review.
- Grier, C. C. and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecological Monographs* 47:373-400.
- Grier, C. C. and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: Relation to site water balance. *Ecology* 58: 893-899.
- Highsmith, R.M. Jr. (ed). 1973. *ATLAS of the Pacific Northwest*. Oregon State University Press, Corvallis. 128pp.
- Johnson, A. H., and T. G. Siccama. 1983. Acid deposition and forest decline. *Environ. Sci. and Technol.* 17:294-299.
- Johnson, A. H., and T. G. Siccama. 1984. Decline of red spruce in the northern Appalachians: Assessing the possible role of acid deposition. *TAPPI Journal* 67:68-72.

- Krause, G. H. M., B. Prinz, and K. D. Jung. 1983. Forest effects in West Germany. pp. 297-332, *In* Davis, D.D., A.A. Millen and L. Dochinger (eds.), *Air Pollution and Productivity of the Forest*. Izaak Walton League and Pennsylvania State University.
- Lassoie, J.P., T.M. Hinckley, and C.C.Grier. 1985. Coniferous forests of the Pacific Northwest. pp. 127-161, *In* Chabot, B.F., and H.A. Mooney (eds.), *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York.
- Morrison, I. K. 1984. Acid rain: A review of literature on acid deposition effects in forest ecosystems. *Forest Abstracts* 45:483-506.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164: 262-270.
- Prinz, B., G. H. M. Krause, and H. Stratman. 1982. *Forest damage in the Federal Republic of Germany*. LIS Report No. 28. Land Institute for Pollution Control, Landesanstalt für Immissionsschutz des Landes Nordrhein-Westfalen. Esse. Wallneyer Strabe 6, Federal Republic of Germany. 145 pp.
- Sprugel, D.G. 1984. Density, biomass, productivity, and nutrient-cycling changes during stand development in wave-regenerated balsam fir forests. *Ecological Monographs* 54:165-186.
- Sprugel, D. G. 1985. Natural disturbance and ecosystems energetics. pp. 335-352, *In* Pickett and White (eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press.
- Tadaki, Y., A. Sato, S. Sakurai, I. Takeuchi, and T. Kawahara. 1977. Studies on the production structure of forests. XVIII. Structure and primary production in subalpine "dead tree strips" *Abies* forest near Mt. Asahi. *Japanese Journal of Ecology* 27:83-90.
- Yarie, J. and K. Van Cleve. 1983. Biomass and productivity of white spruce stands in interior Alaska. *Canadian Journal of Forest Research* 13:767-772.

Selecting Analysis Procedures For Exogenous Disturbance Tree-Ring Studies

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Abstract

Analysis procedures used in dendroecological studies are commonly selected from techniques developed for dendroecological analysis. These techniques, however, are usually limited by factors such as software availability and prior usage. Furthermore, the relationship between the objectives of dendroecological study and the analysis technique is often poorly defined. Conclusions from study objectives, data characteristics, and exogenous disturbance expression indicate that detecting and characterizing nonstationary behavior is the most important ability of the analysis procedure for dendroecological studies. Analysis techniques using constant parameter models do not have this ability. Recursive least squares techniques are promising, but will need further development.

Introduction

Acid deposition, ozone damage, and carbon dioxide increases have focused forest condition questions on the estimation of growth changes through time, and over regions. The data needed to address these questions often must start 50 to 100 years prior to the time of the study.

Traditionally, fixed plot measurements have been used to assess forest condition. These data, however, are rarely of sufficient length, or are available only for local areas. The data sets often are small and contain unknown measurement resolution.

Tree-ring series represent an alternative. Tree cores carefully collected provide inexpensive, highly accurate information on the forest condition. They are inexpensive to collect and process. As many as 1500 cores can be collected, read, and cross-dated in a single year by small research groups. Core reading and cross-dating systems are computerized for consistency and accuracy.

The consistency of data gathering and processing is offset by the confusion and disagreement on analytical techniques useful for this data. Historically, analysis techniques for tree-ring data have been developed to isolate signals, or patterns of tree-ring growth that reflect information pertaining to environmental disturbances, rather than forest condition. Attempts have been made to adapt these techniques to forest condition questions, but the results have been questionable. Most of these analysis procedures examine only the short-term variability (residuals determined by sub-

tracting or dividing the observed ring width values by smoothed values) of the series. Growth changes expressed in the smoothed trend portion of the tree-ring series are often neglected.

Some researchers have proposed new techniques in favor of the traditional techniques (Vissar and Molenar, 1986; Van Deusen, 1986; Peterson and Arbaugh, 1988). These new techniques relax the assumption of constant parameters for the model, which allows evolving systems to be modeled. The techniques have been used in a few studies, but mostly as a slight modification of dendrochronological techniques (Vissar and Molenar, 1986; Van Deusen, 1986). The analysis techniques are also complicated to use and interpret.

The lack of a clear connection between statistical attributes of the analysis process chosen and the study objectives is a major problem for this field. Often, the relationship between the analysis technique and the study objective is either missing, or only haphazardly addressed in studies. Techniques commonly selected are due to availability of software, or prior usage. Consequently, conclusions from these studies may be incomplete, dependent on unstated assumptions, or applied to regions not adequately defined or sampled.

This discussion will attempt to motivate some desirable traits of analytical techniques based on the study objectives, analytical characteristics, and the expression of disturbances in tree-ring series. Statistical aspects of tree-ring series and disturbance expression will be examined. The general types of analytical procedures presently used in dendroecological studies will be discussed with reference to the conclusions obtained.

Study Objectives in Dendroecology

Individual tree-ring series contributes information on the onset and extent of individual

tree growth changes through time. Patterns of ring-width increase, decrease and growth interruptions are recorded in these series. Localized factors, site specific factors and regional disturbances may cause observed short- and long-term changes in growth.

Groups of tree-ring series contribute information on changes in tree growth for sites and regions. The observation of synchronous changes in many series from an area, not observed in past portions of the series or in groups of series from other areas, can be used to infer regional environmental disturbances on tree growth.

The region, or population, that the sample trees represent are dependent upon the sampling strategy used. Sample trees growing without competition in exposed locations can only yield information about trees growing in exposed locations. Meaningful extrapolation of the results to a more general forest population may not be possible. Similarly, sampling interior forest trees will yield information on the majority of trees in the region of interest, but not the trees most likely to be affected by the disturbance.

The growth changes of interest are defined by the objectives of the study. Changes in short-term variability have been the focus of the dendrochronological studies. Associations with climatic changes or exogenous event times often are the primary goals. Studies seek to characterize the event or pattern of events by its expression in tree-ring series.

Studies concerned with assessing forest condition have different goals. In these studies, tree-rings are used as growth indicators to assess regional trends and changes in forest growth. Characterizing stand condition, assessing the effect of known disturbances, and evaluating the impact of growth changes on stand composition for sites and regions are the primary study objectives.

Characteristics of Tree-Ring Series

Characteristics of the data being analyzed are important for selecting an analytical technique. Tree-ring series are particularly difficult in this way. Each series is an equally spaced discrete time series. They are nonperiodic and nonstationary through time. The first moment of the distribution function of the observations may be nonstationary, the mean growth changing through time, or the second central moment may change through time indicating the presence of heteroscedasticity in the data, or both moments may vary through time. For most analysis purposes, these two central moments are the most important. Series with stationary first and second moments are said to be weakly stationary.

The nonstationarity may arise from a variety of causes. Natural disturbances in the environment, gradual biological aging processes and management practices may all be contributing factors. An additional nonstationarity, due to taking linear measurements on a concentrically increasing system, is present if growth is expressed as tree-ring widths.

To simplify the discussion, tree-ring series are assumed to be composed of two components, the long-term trend and the short-term variability. Long-term trend is defined as the smoothed estimates of ring-area values through time. It can roughly be thought of as the nonstationarity of the first moment of the distribution function of the observations. Short-term variability is defined as the residuals formed from differencing (or dividing) the smoothed and actual ring-area estimates. They form a process with a stationary first moment. Nonstationarities in these series are expressed as heteroscedasticity.

Disturbance Expression

A disturbance, endogenous or exogenous, affecting tree growth can be expressed in indi-

vidual tree-ring series in several ways. It may cause a gradual or abrupt change in long-term trends without a corresponding change in the short-term variability. It may cause a change in the short-term variability either relative to environmental factors, or to previous growth without a change in the trend. Combinations trend and short-term variability may also occur. Fluctuations in both the trends and short-term variability are common in tree-ring series.

The particular disturbance expression, or disturbance onset, may be modified for individual trees by interacting influences unique to the tree or site locality. Microclimate, soil characteristics, genetics, or topography may influence individual or site expression of the disturbance.

It is believed that concentric growth is not a stationary process for some species (D. L. Peterson, personal communication). Rather, growth rapidly increases, then becomes stationary or slightly decreasing for a longer period, then decreases more rapidly as the tree ages. It is unknown if short-term variability in concentric growth also varies with time.

Trend changes, both abrupt and gradual, were observed with little evidence of change in short-term variability in forest interior trees sampled in the Sierra Nevada (Peterson and Arbaugh, 1988). Changes in short-term variability were observed when little change in the trend was present. Synchronous changes of the trend and short-term variability were often observed.

Selecting Analytical Methodologies

A tree-ring series is a process evolving through time. Disturbances are expressed as changes, abrupt or gradual, in this process. The ability to characterize the nonstationary aspects of the series, thus, becomes an important characteristic of an adequate analysis procedure. Detecting the time, and the extent of change in both long-term trends and short-term

variability are the primary objectives of the analysis. Without this information, the association of tree-ring patterns with exogenous disturbances is not possible.

If time is available, all types of nonstationary behavior could be examined. This would ensure the detection of disturbance effects expressed in the series that, while not obviously causing a long-term growth decline, could be altering the composition of the forest affected. The analysis might be accomplished using a single technique, or by utilizing several techniques, each for a different aspect of the data.

This would be an exhaustive process, and might be impractical for large studies. At present, prioritization of the importance of the nonstationarities may be necessary. Little information is available pertaining to the pattern of exogenous disturbance expression in individual series, nor is information available indicating the uniqueness of such signals. If such information were available, it might considerably shorten the analysis process.

Obviously, techniques which *a priori* assume that parameters are constant through time will not be effective for this type of analysis, since nonstationary changes in the series could not be isolated. Unfortunately, this includes the majority of techniques developed for dendrochronological analysis. These analytical techniques consist of ordinary least squares multiple regression, principal components regression, ARIMA, or a mixture of techniques. All these techniques assume that the time series is weakly stationary, which precludes estimating nonstationaries in even the short-term variability.

Alternate techniques such as intervention detection and analysis (Box and Jenkins, 1976), and switching regressions (Goldfeld and Quandt, 1973) can be used to compensate for these deficiencies when simple nonstationary trends are present. They are not capable of modeling

all types of nonstationary trends, or heteroscedasticity in short-term variability (without introducing arbitrary power transformations).

More recently, the Kalman filter (Kalman, 1960; Kalman and Bucy, 1961) analysis technique was introduced to dendrochronology (Visser and Molenar, 1986; Van Deusen, 1986). This general class of techniques assumes that model parameters evolve through time according to a function of past parameter values. The simplest form of this transition function, the random walk, is presently utilized in most analysis.

Because the parameters are allowed to vary with time, this class of model is able to track changes in trends, and in short-term variability. Both linear regression models and ARMA model formulations can be constructed for use with this technique. Recursive least squares is also easily extrapolated to the multivariate case.

Although this class of techniques is promising, several general problems exist. Prior to using the model, several parameters and variances must be estimated. There is little consensus on how this is best done. The form of the parameter transition equation must be selected. The simpler forms are easily estimated; however, they restrict the rate of parameter change more than may be desired.

Statistical inference procedures are largely undeveloped for the Kalman filter. This reduces study conclusions to the interpretation of parameter values or confidence intervals based on expert knowledge of the system rather than distributional results.

Recursive least squares procedures are also more complex, less available in standard analysis packages, and more difficult to interpret than the stationary models. Only one study has applied this to the trend portion of the series (Peterson and Arbaugh, 1988). Additional studies using this technique by other researchers

are needed before its strengths and limitations will be completely known.

Recursive least squares is a promising technique. The difficulties in application and interpretation can be addressed with further research. However, additional analysis techniques need to be developed as alternatives. Reliance on a single technique could restrict the types of information that can be obtained from tree-ring series. Future techniques might include process oriented models, different statistical analysis procedures, or even an expert system approach.

New conceptual approaches to analysis might also be possible. One such approach might be to consider both the long- and short-term variability as a single pattern of growth. Patterns associated with exogenous influences could then be identified by control studies, or sensitive series, and used to identify patterns of interest in interior forest trees. This could reduce the analysis time and the uncertainty of results.

In summary, the primary analysis goal is the detection of nonstationary behavior in the tree-ring series when detection of the expression of cumulative exogenous disturbances in tree-ring series is the study objective. This will consist of examining the long-term trends and short-term variability for points or patterns of change. Techniques developed for dendrochronological analysis are generally not adequate, since they examine short-term variability exclusively, and assume parameter to be con-

stant. Recursive least squares techniques are promising, but will need more refinement before being widely applicable. Techniques other than recursive least squares might be developed to give a more balanced approach to analysis efforts in the future.

Literature Cited

- Box, G. E. P., and G. M. Jenkins. 1976. *Time series analysis: forecasting and control*. Holden-day Inc., San Francisco, CA.
- Goldfeld S. M., and R. E. Quandt. 1973. The estimation of structural shifts by switching regressions. *Ann. of Econ. and Soc. Meas.*, 2:475-485.
- Kalman, R. E. 1960. A new approach to linear filtering and prediction problems. *Trans. ASME J. Basic Engrg.* (ser. D) 82:35-45.
- Kalman, R. E., and R. S. Bucy. 1961. New results in linear filtering and prediction problems. *Trans. ASME J. Basic Engrg.* (Ser. D) 82:35-45.
- Peterson, D. L., and M. A. Arbaugh. 1988. *Growth trends in the mixed conifer forest of the Sierra Nevada: A final report*. Report to Western Conifers Research Cooperative, EPA, Corvallis, OR.
- Van Deusen, P. C. 1986. Some applications of the Kalman filter to tree-ring analysis. In: *Proc. International Symposium on Ecological Aspects of Tree-Ring Analysis*. Lamont-Dohert Geological Observatory, Columbia Univ., Palisades, NY.
- Visser, H., and J. Molenaar. 1986. *Time dependent responses of trees to weather variations: an application of the Kalman filter*. N. V. Tot Keuring Van Elektrotechnische Materialen, Research and Development Division, Arnhem, The Netherlands.

Session

II

Mechanisms and Alternative Hypotheses

Ann Bartuska, Local Organizer

Introduction

While research on air pollution effects on plants has been conducted in the United States for 2 decades, it has only been in the last 5 years that a coordinated National effort has been pursued. A principal focus of this effort has been understanding the mechanisms of response at the whole plant, organ and cellular levels. Studies of mechanisms of response have been an area of research in the Soviet Union for many years. Accordingly, the theme of the Raleigh session was "Mechanisms and Alternative Hypotheses" with a subtheme of "Linkages: Seedlings vs Trees vs Ecosystems."

Each day of the 2-day session began with a series of formal presentations, followed by workshop-format discussions developed from the formal presentations. Presentations from both countries were very complementary, covering the entire range of mechanisms from ultrastructural changes due to SO₂, to forest structural changes as a result of ambient environmental conditions. In total, 14 presentations and 20 scientific posters greatly stimulated discussions regarding the differences in the pollutant environment and the similarity in affected processes between the two countries.

Ann Bartuska

Air Pollutants, Plants, and Mechanisms of Interaction: A Historical Perspective*

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This paper was designed to provide a brief historical perspective on scientific research on the interactions between airborne pollutant chemicals and both crop and forest plant species. The two of us have been engaged in air pollution research in the United States for a combined total of nearly 50 years. Based on this experience, we have developed a few perspectives which we share with other participants in this USA-USSR Workshop. We hope these ideas will be of some value in encouraging a more complete understanding of the interactions between plants and airborne pollutant chemicals in our two countries.

Our paper is organized in three parts:

- A summary of general trends in scientific understanding
- A list of major conclusions regarding effects of air pollutants on crop and forest

- plant species in the United States
- A 'Literature Cited' list which contains some of the most valuable scientific reviews and original papers dealing with air pollution research in North America.

General Trends in Scientific and Technical Understanding

Scientific understanding of the interactions between phytotoxic air pollutants and both agricultural crops and forest vegetation in Europe (including the Soviet Union) and the United States has evolved mainly during the 20th century. Eville Gorham (NRC, 1981) has given an excellent summary of early European and North American developments in scientific understanding of plant-atmosphere interactions. Gorham's summary clearly shows that severe air pollution problems were addressed in the 19th century.

*Keynote paper presented by Dr. Cowling on September 19, 1988

Crocker (1948) and Thomas (1951, 1961) have given similarly valuable accounts of studies of air pollution injury to vegetation near the metal smelters at Selby, California; Copper Hill, Tennessee; and Salt Lake City, Utah in the United States and at Sudbury, Ontario in Canada. Katz (NRC of Canada, 1939) has also given a remarkably detailed account of the observational and experimental investigations during the most intensively studied of these early smelter release problems—the case of plant injuries caused by sulfur dioxide emissions from the smelter at Trail, British Columbia. This latter case-study led to the formation of the International Joint Commission which has helped resolve transboundary air pollution conflicts between Canada and the United States for nearly 50 years.

These early investigations were based mainly on field surveys of direct injury to foliage of both crop plants and natural vegetation. The injuries were induced by toxic gases dispersed in the immediate vicinity of strong point sources—mainly metal smelters. Sulfur dioxide and later fluoride were the principal pollutants of concern (NCR of Canada, 1939; Crocker, 1948; Thomas, 1951; Brandt and Heck, 1967; NRC, 1981; Shupe, 1983). Although measurements of air pollution concentrations were very crude at first, both pollutant-monitoring methods and equipment for controlled exposures with known concentrations of these toxic gases became progressively more sophisticated during the early decades of this century (NRC of Canada, 1939; Crocker, 1948; Thomas, 1969).

Controlled exposures with known concentrations of specific pollutants in greenhouse chambers were first used to quantify suspected pollutant dose/plant-response relationships (Crocker, 1948). Later, closed field chambers, then open-top field chambers, both using charcoal-filtered air as a control, were used with ambient air augmented with controlled additions of specific pollutants to quantify dose-response relations. Continuous stirred tank

reactor (CSTR) chambers were developed for studying physiological effects under greenhouse and controlled environment conditions (Heck *et al.*, 1978). Pollutant-specific bioindicator plants were also developed to augment field observations (Heck, 1966; Heck and Heagle, 1970).

During the late 1940's and early 1950's, photochemical oxidants, especially ozone and later peroxyacetyl nitrate (PAN) were shown to be highly toxic constituents of the smog for which the Los Angeles area of southern California has become famous (Haagen-Smit, 1952; Haagen-Smit, *et al.*, 1953). These substances were soon discovered to be highly toxic to plants as well as humans. We now recognize that ozone is one of the most common toxic gases that affect plants in fields and forests in many parts of the world (Middleton, 1961; NRC, 1977b; EPA, 1986).

During the early 1950's, power plants were shown to be sources of phytotoxic air pollutants (especially sulfur dioxide), and they also contributed to the mix of volatile organic compounds and nitrogen oxides that lead to formation of ozone and other photochemical oxidants (Brandt and Heck, 1967; NRC, 1977b; EPA, 1973).

Gaseous nitrogen oxides have been shown to cause foliar injury to some crop plants and forest trees in controlled exposure tests both alone and in combination with other toxic gases. But important injuries at ambient concentrations have not been observed in either fields or forests in North America (NRC, 1977c; EPA, 1982).

At present, the airborne chemicals known to affect vegetation in the field include sulfur dioxide, fluoride, ozone, PAN, chlorine, hydrogen sulfide, ammonia, aniline, ethylene, and aerosols containing herbicidal chemicals (Crocker, 1948; Brandt and Heck, 1967; Jacobson and Hill, 1970). Much of the available information on the effects of these air pollutants

is summarized in the so-called Criteria Documents used by the Environmental Protection Agency of the United States in establishing the air quality standards for this country (EPA, 1973, 1982, 1986). Table 1 contains a composite of the threshold doses (air concentration and time of exposure) necessary to induce visible injury by sulfur dioxide, nitrogen oxides, and ozone. The data shown are for a variety of crop plants that are sensitive, intermediate, and tolerant of each of these major pollutants (EPA, 1973, 1982, 1986).

During the 1970's and 1980's, extensive research on the phenomenon and effects of acid deposition has been done in North America. This research has included studies of the emission, transport, deposition, and biological effects of acidic substances including gases, aerosols, and acidic substances dissolved in precipitation (Cowling, 1985). Cowling (1982) has also prepared a summary of the historical roots of the acid deposition issue in North America and Europe. Effects on the chemistry and biology of surface waters have been documented and both direct and indirect effects on a wide variety of crop and forest plants have been studied. Present evidence suggests that effects on agricultural crops and forest trees are mediated mainly through interference with nutrient uptake processes or aluminum toxicity in soils rather than by direct toxicity to foliar organs (NAPAP, 1987).

The physiological and biochemical mechanisms by which air pollutants injure plants are still poorly understood. Stomata on foliage and stem surfaces have been shown to be the principal avenue of entrance of gaseous pollutants into plants (NRC 1977a, 1977b, 1977c; EPA 1973, 1982, 1986). Differences in stomatal behavior may account for an important part of the natural variation observed in plant resistance or susceptibility to most gaseous pollutants. Sulfur dioxide, fluoride, ozone, and nitrogen oxides all appear to be general metabolic poisons that disrupt cell membranes

and interfere with a wide array of metabolic processes in plants (NCR 1977a, 1977b, 1977c; EPA 1972, 1982, 1986; Shupe *et al.*, 1983).

In the United States, recent studies of the economic impact of air pollutants indicate that injury by locally dispersed sulfur dioxide and fluoride are now very rare and that regionally dispersed ozone is the principal air pollutant of concern (Heck *et al.*, 1986). Decreases in emissions of volatile organic compounds (VOCs) from industrial and commercial sources are the principal control strategy for ozone. Very recent studies indicate that this policy is not adequate in the southern United States. Here, natural emissions of VOCs from forest and crop plants are so large that it probably will be necessary also to limit emissions of nitrogen oxides if ambient concentrations of ozone are to be maintained below phytotoxic concentrations.

In the Soviet Union, locally dispersed sulfur dioxide and fluoride continue to be of concern in some heavily industrialized areas. Here, significant progress is being made in the development of crop varieties and forest trees that are resistant to gaseous pollutants or can produce reasonable yields under prevailing pollutant loads.

Major Conclusions Regarding Effects of Air Pollutants on Vegetation in North America.

The major conclusions enumerated below were developed as a synthesis of about 60 years of experience in research on the effects of air pollutants on plants in the United States.

- 1) Ozone is responsible for most of the crop-yield losses from air pollutants on both a regional and national scale within North America.
- 2) Losses from other pollutants are minimal, relative to ozone, and primarily occur very close to sources, or are induced by joint effects with ozone.
- 3) Ozone may be the most important cause of air pollution injuries in forests in the United

Table 1. Critical concentrations of gaseous pollutants that induce visible injury to vegetation in Eastern North America (all concentrations are in ppm).

Time of Exposure (hours)	Sulfur Dioxide ¹			Nitrogen Dioxide ²			Ozone ³		
	Sensitive	Intermediate	Tolerant	Sensitive	Intermediate	Tolerant	Sensitive	Intermediate	Tolerant
0.5	1.0 - 4.0	3.5 - 12.0	>10.0	6.0 - 10.0	9.0-17.0	>16.0	0.35-0.50	0.55-0.70	>0.7
1.0	0.5 - 3.0	2.5 - 10.0	> 8.0	4.0 - 8.0	7.0-14.0	>13.0	0.15-0.25	0.35-0.40	>0.4
2.0	0.25- 2.0	1.5 - 7.0	> 6.0	3.0 - 7.0	6.0-12.0	>11.0	0.09-0.15	0.15-0.25	>0.3
4.0	0.1 - 1.0	0.5 - 5.0	> 4.0	2.0 - 6.0	5.0-10.0	> 9.0	0.04-0.09	0.10-0.15	>0.25
8.0	0.05- 0.5	0.2 - 2.5	> 2.0	2.0 - 5.0	4.0- 9.0	> 8.0	0.02-0.04	0.07-0.12	>0.2

¹EPA 1973.
²EPA 1982.
³EPA 1986.

States and Canada. Strong evidence has been obtained for foliar injury by ozone to white pine and many other conifer and hardwood tree species in large parts of eastern North America. In southern California, ozone can predispose forest tree species to attack by bark beetles and root-rotting fungi and, thus, can cause important changes in the species composition of forests. Although foliar injury to individual trees is well documented in many tree species, losses in productivity of whole forests has not been demonstrated in North America (Woodman and Cowling, 1987).

4) Mathematical response functions that relate pollutant dose to crop yield are essential for predicting yield losses in agricultural crops; nonlinear models give the best fit to available field data for ozone.

5) A descriptive analysis of regional variation in ozone concentration using a kriging technique is a useful and necessary part of economic assessment efforts. These same techniques are not suitable for sulfur dioxide or other point-source related pollutants.

6) Foliar symptoms on agricultural crops under field conditions often are similar to early senescence. For this reason, they are often difficult to quantify.

7) Although the physiological and/or biochemical mechanisms of plant response to most air pollutants are not well understood, cell membranes appear to be a principal site of initial impact in the case of ozone.

8) Both ozone and sulfur dioxide affect photosynthesis and carbon allocation; decreased allocation of carbon to root and reproductive structures is common. Similar physiological mechanisms may also be involved in interactions between plants and other gaseous pollutants.

9) Synergistic interactions in the effects of ozone, sulfur dioxide, nitrogen oxides, and fluoride have been documented in a number of species of crop plants.

10) Interactions are also known to occur between air pollutants and other abiotic stresses such as water stress and nutrient deficiencies,

and biotic stresses such as pathogens and insects.

11) Most agricultural crops show decreases in growth, biomass, and yield when the crops are grown under air concentrations of these pollutants that are commonly found in the eastern United States and Canada.

12) The data on agricultural crop losses, accumulated in connection with the National Crop Loss Assessment Network (NCLAN), has given a reasonable first estimate of ozone-induced injury to crop production in the United States. The total economic value of these losses on the most important crops of the United States are estimated to be from \$1 to 5 billion annually. If known damage induced by ozone on less important crops were added, the total economic impact of tropospheric ozone on agricultural crop production in this country could be as high as \$7 billion annually. Changes in meteorological conditions from year to year is the principal source of annual variations in the economic impact of ozone.

Literature Cited

- Brandt, C. S., and W. W. Heck. 1967. Effects of air pollutants on vegetation. pp. 401-443, *In* Stern, A.A. (ed.), *Air Pollution. Volume 1*. Academic Press, New York.
- Crocker W. 1948. *Growth of Plants: Twenty Years' Research at Boyce Thompson Institute*. Rheinhold Publishing Co., New York. 459 pp.
- Cowling, E. B. 1982. Acid precipitation in historical perspective. *Environmental Science & Technology* 16:110A-123A.
- Cowling, E. B. 1985. Pollutants in the Air and Acids in the Rain: Influences on our Natural Environment and a Challenge for Every Industrial Society. XXVth Horace M. Albright Conservation Lecture, College of Natural Resources, University of California, Berkeley, California. 26 pp.
- Environmental Protection Agency. 1973. *Air Quality Criteria for Sulfur Oxides*. EPA-R3-73-030. National Environmental Research Center, Research Triangle Park, North Carolina.

- Environmental Protection Agency. 1982. *Air Quality Criteria for Nitrogen Oxides*. EPA-600/8-82-026. National Environmental Research Center, Research Triangle Park, North Carolina.
- Environmental Protection Agency. 1986. *Air Quality Criteria for Ozone and other Photochemical Oxidants*. EPA-600/8-84-0200F. National Environmental Research Center, Research Triangle Park, North Carolina.
- Haagen-Smit, A. J. 1952. Chemistry and physiology of Los Angeles smog. *Industrial & Engineering Chemistry* 44:1342-1346.
- Haagen-Smit, A. J., C. E. Bradley, and M. M. Fox. 1953. Ozone formation in photochemical oxidation of organic substances. *Industrial & Engineering Chemistry* 45:2086-2089.
- Heck, W. W. 1966. The use of plants as indicators of air pollution. *Air & Water Pollution International Jour.* 10:99-111.
- Heck, W. W., and A. S. Heagle. 1970. Measurement of photochemical air pollution with a sensitive monitoring plant. *Journ. Air Pollution Control Assoc.* 20:97-99.
- Heck, W. W., A. S. Heagle, and D. S. Shriner. 1986. Effects on vegetation: Native, crops, forest. pp. 247-350, *In: Stern, A.A. (ed), Air Pollution, Vol. 6*. Academic Press Inc., New York, New York.
- Heck, W. W., S. V. Krupa, and S. H. Linzon, eds. 1979. *Handbook of Methodology for the Assessment of Air Pollution Effects on Vegetation*. Upper Midwest Section, Air Pollut. Control Assoc., Specialty Conference Proceedings. April 1978. 392 pp.
- Jacobson, J. S., and C. Hill, eds. 1970. *Recognition of Air Pollution Injury to Vegetation: A Pictorial Atlas*. Air Pollution Control Assoc. Pittsburgh, Pennsylvania. 90 pp.
- Middleton, J. T. 1961. Photochemical air pollution damage to plants. *Annual Review Plant Physiology* 12:431-448.
- National Acid Precipitation Assessment Program. 1987. Interim Assessment: *The Causes and Effects of Acidic Deposition*. Volumes I, II, III, and IV. Council on Environmental Quality, Washington, DC.
- National Research Council. 1977a. *Fluorides*. National Academy Press, Washington, DC. 295 pp.
- National Research Council. 1977b. *Ozone and Other Photochemical Oxidants*. National Academy Press, Washington, DC. 718 pp.
- National Research Council. 1977c. *Nitrogen Oxides*. National Academy Press, Washington, DC. 333 pp.
- National Research Council. 1981. *Atmosphere-Biosphere Interactions: Toward a Better Understanding of the Ecological Consequences of Fossil Fuel Combustion*. National Academy Press, Washington, DC. 263 pp.
- National Research Council of Canada. 1939. *Effect of Sulphur Dioxide on Vegetation*. National Research Council of Canada, Ottawa, Canada. 447 pp.
- Shupe, J. L., H. B. Peterson, and N. C. Leone. 1983. *Fluorides: Effects on Vegetation, Animals, and Humans*. Paragon Press, Salt Lake City, Utah. 369 pp.
- Thomas, M. D. 1951. Gas damage to plants. *Annual Review Plant Physiology* 2:293-322.
- Thomas, M. D. 1961. *Effects of Air Pollution on Plants*. Air Pollution. World Health Organization Monograph Series 46:233-278.
- Thomas, M. D. 1969. *Photochemical smog*. Air Quality Monograph 69-6. American Petroleum Institute, New York. 40 pp.
- Woodman, J. N., and E. B. Cowling. 1987. Airborne chemicals and forest health. *Environmental Science & Technology* 21:120-126.

The Impact of Sulfur Dioxide Fumigation on Photosynthetic and Ultrastructural Responses of Mesophyll Cells from Developing *Pinus strobus* Needles. 1. Mesophyll Cells

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Abstract

Two-year-old eastern white pine (*Pinus strobus*) seedlings were fumigated with sulfur dioxide (SO_2) two hours each day for five days during the time of new needle emergence. The needles from the SO_2 -treated plants were shorter than controls, but otherwise showing no macroscopic signs of damage. Photosynthetic measurements taken during the times of fumigation showed a steady decline during each two hour exposure to SO_2 , and a reduced level of activity on each succeeding day of the experiment. Ultrastructural studies revealed three stages of degradation which were consistent among cells throughout the young needles. Special attention was directed at the degradation of chloroplasts, mitochondria, peroxisomes, ribosomes and nuclei. The ultrastructural changes are related to recorded changes in size and photosynthetic activity of the needles, and shows that severe microscopic and physiological damage may be present before obvious macroscopic damage is evident.

Introduction

This study seeks to reveal specific physiological and ultrastructural responses in the mesophyll cells of developing pine needles prior to visible damage when fumigated with sulfur dioxide (SO_2). These changes are documented both by means of transmission electron microscopy, and by measurements of carbon dioxide utilization. It may be noted that in recent years, there have been several studies of gymnosperm foliar structures in which the plants have been exposed to SO_2 (Smith and Davis, 1978; Soikkeli, 1981; Soikkeli and Tuovinen, 1979; von Parameswaran *et al.*, 1985; Soikkeli, 1981). However, most studies have been directed specifically at the structural responses of chloroplasts to atmospheric pollutants (e.g. Malhotra, 1976; Soikkeli, 1981). Little attention has been directed towards the responses of other cellular components to the influence of air pollutants, and no reports are known regarding the specific effects on nuclear structures. This study, therefore, is directed at varied aspects of the ultra-

structural response of *Pinus strobus* mesophyll cells to SO₂ fumigation with regard to the photosynthetic responses during experimental fumigation.

Materials and Methods

Two-year old seedlings of eastern white pine (*Pinus strobus*) were grown in soil under greenhouse conditions and, in mid-spring (April), representative plants were introduced into environmental chambers illuminated with 300 $\mu\text{E}/\text{m}^2/\text{sec}$ (slightly red) light, at 53-58% relative humidity, and at a temperature of 23°C ($\pm 1^\circ\text{C}$). Plastic bags were tied around the pots to the stems of the plants in order to prevent SO₂ absorption into the soil which might affect respiratory measurements. Carbon dioxide (CO₂) levels were monitored continuously during each two hour experimental period using a Beckman infra-red gas analyzer. The measure of CO₂ consumed at the end of each 24 minute period over the course of the two hours as a function of the total needle dry weight of the plants, became a measure of the photosynthetic capacity of the plants for each day. Dry weights were taken of all green needles at the conclusion of the experiment on the fifth day. For the control plants, the average wet and dry weights of the needles were 14.92 g and 5.68 g respectively, and for the experimental material, the values were 14.15 and 5.47 g respectively.

In the experimental chamber, atmospheric SO₂ was maintained at 1.0 ppm for two hours each day over the course of five days. The control chamber was maintained under identical conditions except for the presence of only ambient levels of SO₂ (0.03 — 0.05 ppm). At the end of 3 and 5 days, small segments of the newly-developing needles were taken from their tips and from their bases for electron microscopy fixation. Segments as similar as possible were prepared from both experimental and control plants. The fixation procedure was conventional for the ultrastructural preservation of plant material except that 1.0% caffeine was added to the initial (glutaraldehyde) fixative in

order to prevent the leaching of vacuolar tannins into cytoplasmic structures (Mueller and Greenwood, 1978). The samples were dehydrated in a graded ethanol series and embedded in a Spurr-Epon resin mixture. Sections were stained with lead citrate and subsequently examined with a Hitachi H-600 transmission electron microscope operating at 75 kv.

Results and Discussion

Following either three or five days of SO₂ fumigation, the newly-expanding needles on the exposed plants showed no visible macroscopic damage. However, needles from the SO₂-fumigated plants were demonstratively shorter at the end of the five day period than the corresponding control needles (Fig. 1). Whereas the average length of control needles was 26.0 mm, the needles from fumigated plants were 5-6 mm shorter.

Figure 2 shows the CO₂ uptake in control and SO₂-treated pine plants as a function of the total needle dry weight. Control ratios varied between 6.7 and 7.1 $\mu\text{g CO}_2$ uptake/g dry weight, but very large differences were noted in the SO₂-treated plants. The results showed a general decline in the starting photosynthetic levels each day over the course of the five day fumigation period, indicating that there is a certain amount of accumulative permanent damage to the photosynthetic system which can be carried over from one day to the next. Furthermore, there was a steady decline in photosynthetic activity at each 24 minute time period during the course of the daily two hour experimental exposure to SO₂ fumigation. This was demonstrated by a "leveling-off" of CO₂ consumption to a very low level between 96 minutes and 120 minutes each day. Although the decline in photosynthetic activity each day was rather dramatic, starting levels the following day were always significantly higher than the final measurement of the previous day, indicating that a certain component of the damage was reversible.

While the exposure to SO₂ may have inhibited cellular elongation in the developing needles, our ultrastructural observations indicate that severe damage was occurring. Examination of basal and tip-region plicate mesophyll cells showed similar results in the SO₂-fumigated specimens. The only difference was that similar damage to mesophyll cells was delayed by about two days in the base as opposed to the tip. No observable damage occurred to meristematic cells—even after the full five days of the experiment (compare Figs. 5 and 11). Thus, we presume that SO₂ fumigation did not interfere with mitotic development. The results revealed three stages of cellular degradation in mesophyll cells prior to their complete destruction. A summary of these stages of degradation is presented in Table 1. It is important to note that these stages of cellular alteration and degradation occurred when there was no direct visible damage to the needles. It should also be noted that damage was random throughout the plicate mesophyll with severely damaged cells sometimes adjacent to evidently healthy cells.

The following is a description of the sequential damage which occurred to specific cellular components within the mesophyll tissue from SO₂-treated specimens. Control material remained in a healthy-appearing state, both macroscopically and microscopically, and all following references made to the controls are strictly for comparative purposes.

Chloroplasts within cells showing stage 1 damage were comparable to those of control cells, except that the starch grains were smaller and less abundant (compare Figs. 3 and 9, and Figs. 4 and 10). In sectioned planes, only one or two starch grains could typically be observed in chloroplasts from SO₂-treated specimens, whereas up to one-third of the sectional view of control plastid profiles were occupied by large starch grains. In the early stage of cellular damage, there were no differences noted in the number, size or distribution of plastoglobuli. Small, dense, and often single plastoglobuli could be observed in the chloroplast matrix, and sometimes three to seven could be found in

Table 1. Summary of ultrastructural responses in developing needles of first year growth of SO₂-fumigated *P. strobus*. Changes are noted for the major protoplasmic components of the plicate mesophyll cells.

	Chloroplasts	Mitochondria	Peroxisomes	Ribosomes	Nucleus
Control	Nearly 1/3 starch	Normal	Normal	Free and RER	Large membrane invaginations
Stage 1	Reduced starch	Normal	Matrix translucent	Free and RER	Small membrane invaginations. 1-2 nucleoli.
Stage 2	Thylakoids swollen with dense lumens	Matrix less dense; reduced cristae	Matrix with coagulation	Reduced frequency	No euchromatin. Only nucleolar fibrillar structure.
Stage 3	Only starch and plastoglobuli remain	Matrix transparent; no cristae	Matrix entirely dense	Completely absent	Small nuclei. Heterochromatin reticulum formed.

Complete breakdown with no recognizable morphological structure remaining.

aggregation within a single plastid profile. Likewise, the thylakoid system appeared unchanged between control and experimental specimens with from two to three thylakoids in small grana, and 25 to 30 in large grana (Fig. 6). These, in turn, were oriented towards the vacuolar side of the plastids within a dense stroma that was more prominent on the cell wall side of the plastids. In what may be designated as a second stage of degradation, the thylakoids became greatly swollen and the contents of the thylakoid lumens became more dense (compare Figs. 6 and 12). Starch grains and plastoglobuli persisted in a dense thylakoid-stroma matrix. In the third stage of degradation, the chloroplast integrity was completely destroyed, and its contents became a homogeneous mass in which only starch grains and plastoglobuli could still be identified.

Observations of mitochondria from the first stage of degradation showed no differences from those of the control group. They possessed a circular profile with small granules in the matrix and small cristae. In the second stage, the matrix of most mitochondria became less dense, and the cristae even less prominent (Fig. 13). By the third stage of degradation, the mitochondrial matrix became electron-transparent, and virtually no cristae could be recognized in the remaining organelle profiles. Beyond this stage, it was no longer possible to morphologically identify the mitochondria.

In stage 1, peroxisome profiles were equal, or up to three times greater, in sectional area than those of mitochondria, although the matrix was nearly translucent (similar to Fig. 6). While somewhat larger than mitochondria, there were fewer numbers of these organelles per cell. Typically, only two to four peroxisome profiles could be observed in each section. In a second stage of degradation, the peroxisome matrix began to show coagulation and, in the third stage, electron-dense material occupied nearly the entire content of these organelles. Following this, the limiting membrane was no longer

evident and these organelles could no longer be identified.

In addition to changes in membrane-bound organelles, early alterations of ribosomes could also be observed. In the first stage, both polyosomes and free individual ribosomes were commonly observed. In the second stage, ribosomes of both types were largely lacking, and by the third stage, they were completely absent.

Major attention was directed at changes noted in the nuclear structure. In stage 1, nuclear profiles were circular with occasional small invaginations of the envelope membranes. While otherwise similar, nuclei from control specimens possessed more frequent and longer narrow channels of these invaginations (Figs. 4 and 7). Chromatin in diffuse form (euchromatin) and in condensed form (heterochromatin), appeared rather uniformly dispersed throughout the nuclei. One or two prominent nucleoli could be found in each nuclear profile of control and stage 1 specimens (Fig. 8). These structures possessed large, but not deep, lobes and, at times, nucleolar vacuoles. Both granular and fibrillar components were present with granular ones predominating. By stage 2, the nuclear chromatin was only found in the condensed form with no evidence of euchromatin being present. Only fibrillar structures and irregularly-shaped electron-dense granules remained of the nucleolar structures. In the third stage, the size of the nuclei noticeably decreased. The contents appeared to be comprised of only a reticulum of condensed heterochromatin which possessed a rather "fuzzy" or "melted" appearance (Fig. 14). Following this stage, the remaining nuclear substance became a homogeneous mass of moderately dense material. These changes in nuclear structure during cellular degradation are believed to be related to a great decrease in the biosynthesis of ribosomal RNA as evidenced by the sudden reduction of ribosomes in stage 2.

Thus, even when no visible damage could be observed after five days of SO₂ fumigation, considerable ultrastructural damage could be identified. The needles, while macroscopically appearing healthy, could be shown to have large numbers of mesophyll cells in various stages of damage. Only two of the stages of degradation were found in basal cells as opposed to the needle tip after five days of SO₂ fumigation. Presumably, the same levels of degradation would, in time, occur in the basal mesophyll cells. It is possible that stage 1 of degradation represents the level of damage which is reparable, and which may correspond to the demonstrated recovery in photosynthetic activity from the end of one day's fumigation to the start of the next day's fumigation time. The continuing day-to-day decline in photosynthesis may correspond with the ultrastructural changes shown in stages 2 and 3 and, obviously, in the total destruction of the cells. While no evidence indicates structural damage of the meristematic tissue, the shorter average needle length in the SO₂-fumigated plants (compared with the control) suggests that some of the damage must contribute to the stunted growth of the needles. If the meristem is not directly affected, then an inhibition of cell elongation may be a factor in reduced growth along with the random destruction of mesophyll cells. This study strongly suggests that episodic events of SO₂ pollution in the atmosphere reaching levels of approximately 1.0 ppm may, in a short time, cause significant and lasting damage to pine trees—particularly in new foliar growth.

Acknowledgments

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Literature Cited

- Malhotra, S.S. 1976. Effects of sulfur dioxide on biochemical activity ultrastructural organization of pine needle chloroplasts. *New Phytol.* 76(2):239-245.
- Mueller, W.C., and A.D. Greenwood. 1978. The ultrastructure of phenolic-storing cells fixed with caffeine. *J. Exp. Bot.* 29:757-764.
- Smith, H. J., and D. D. Davis. 1978. Histological changes induced in Scotch pine needles by sulfur dioxide. *Phytopath.* 68(12):1711-1716.
- Soikkeli, S. 1981. Comparison of cytological injuries in conifer needles from several polluted industrial environments in Finland. *Ann. Bot. Fenn.* 18:47-61.
- Soikkeli, S. 1981. The types of ultrastructural injuries in conifer needles of northern industrial environments. *Silva Fennica* 16:399-404.
- Soikkeli, S., and T. Tuovinen. 1979. Damage in mesophyll ultrastructure of needles of Norway spruce. *Ann. Bot. Fennici* 16(1):50-64.
- von Parameswaran, N., S. Fink, and W. Liese. 1985. Feinstrukturelle untersuchungen an nadeln geschadigter jannen und fichten aus waldschadensgebieten im Schwarzwald. Sonderdruck aus *European J. Forest Pathol.* 15(3):168-182.



Figure 1. Comparison of first year needles from fascicles having similar length prior to the fumigation study. The shorter needles are from an SO₂-fumigated *P. strobus* plant. Note millimeter scale.

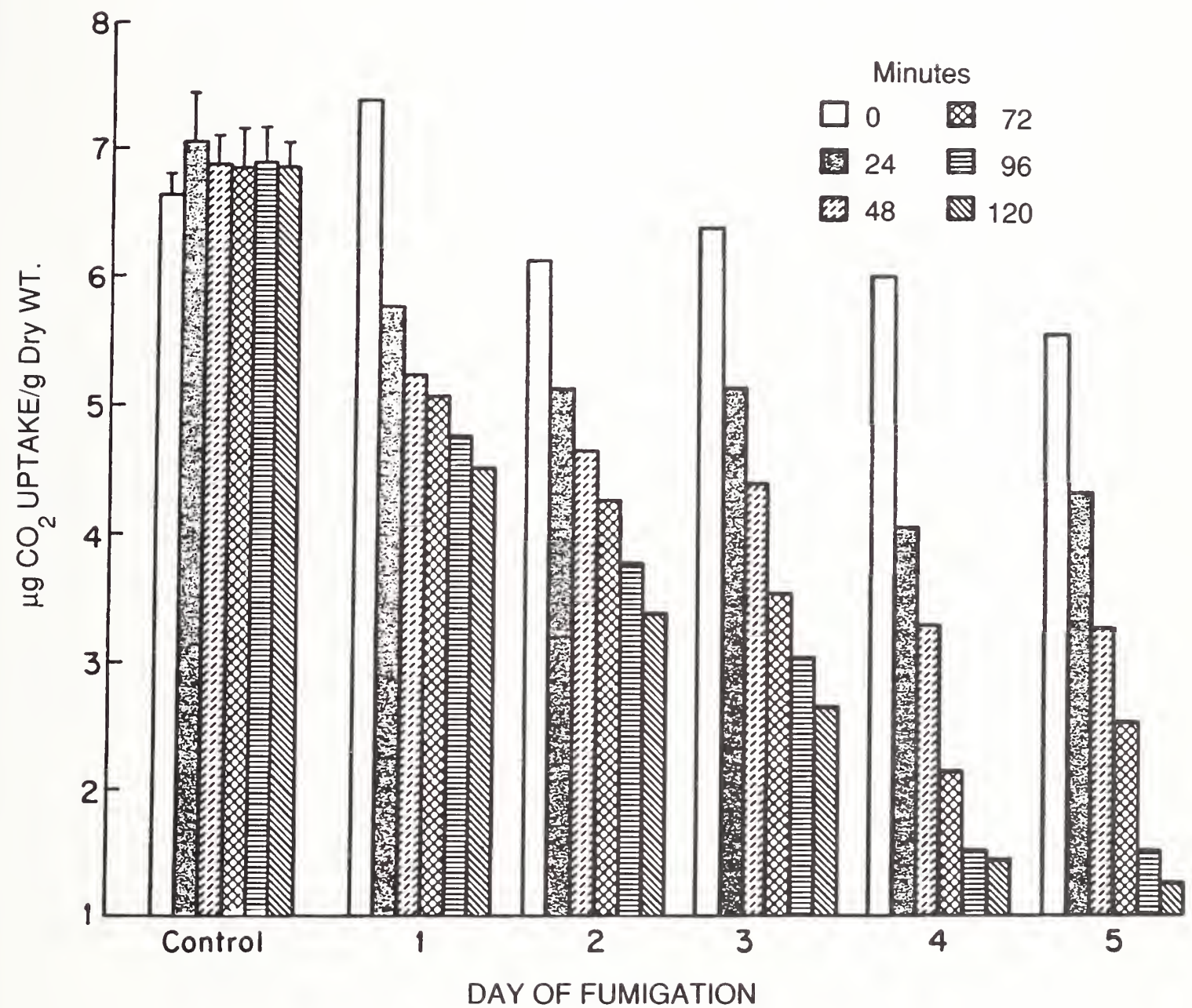
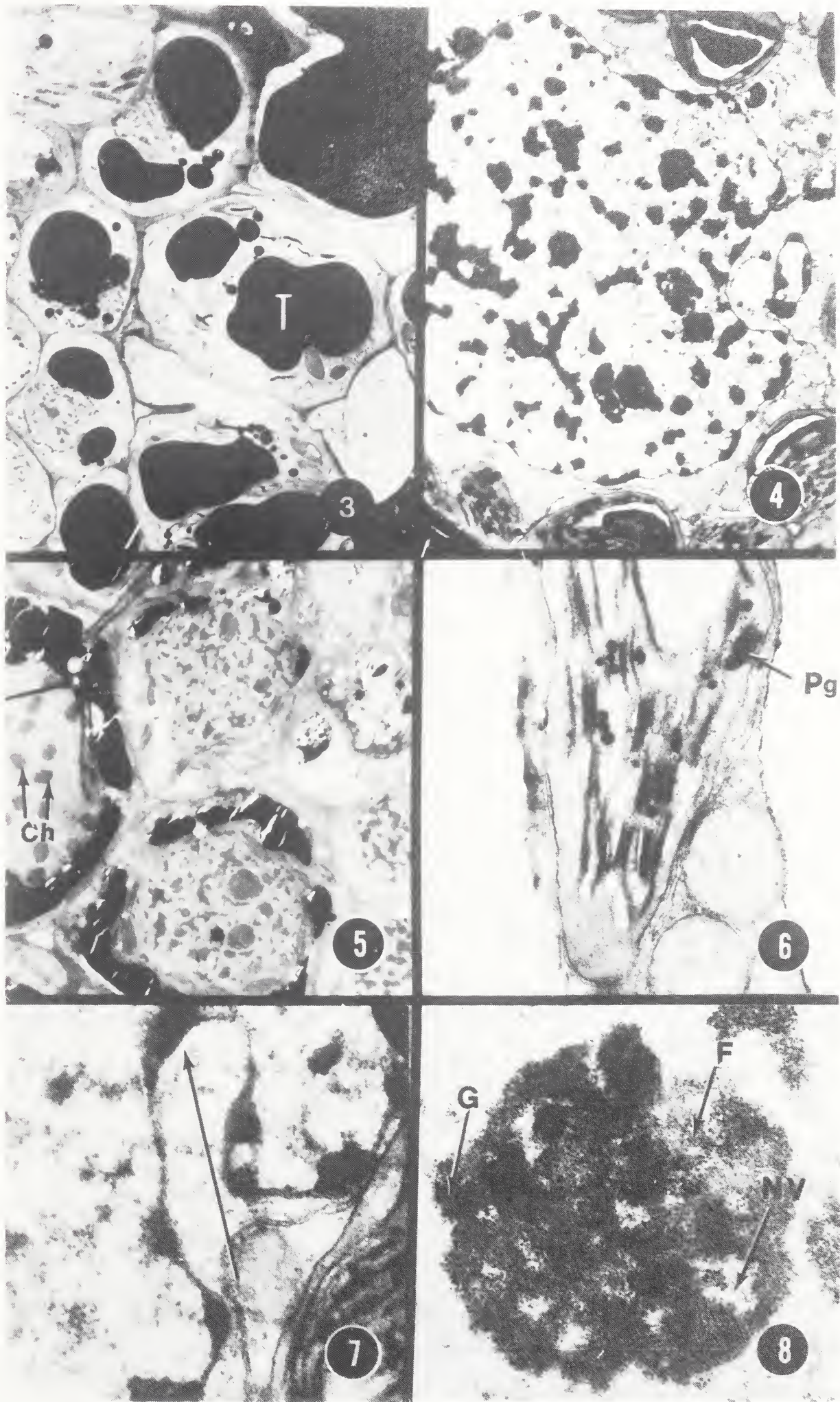


Figure 2. Photosynthesis rates of 0.5ppm SO_2 -treated 2 year-old pine seedlings. Carbon dioxide uptake in control and SO_2 -fumigated *P. strobus* seedlings. Values on the vertical axis represent the numerical ratio of $\mu\text{g CO}_2$ consumed per gm dry weight of green foliar material. Time periods up to 2 hr (120 min) are given on the horizontal axis in which control plants and the experimental plants are compared for each day (days 1-5) Since control values were relatively stable each day, only one set of average values is given.

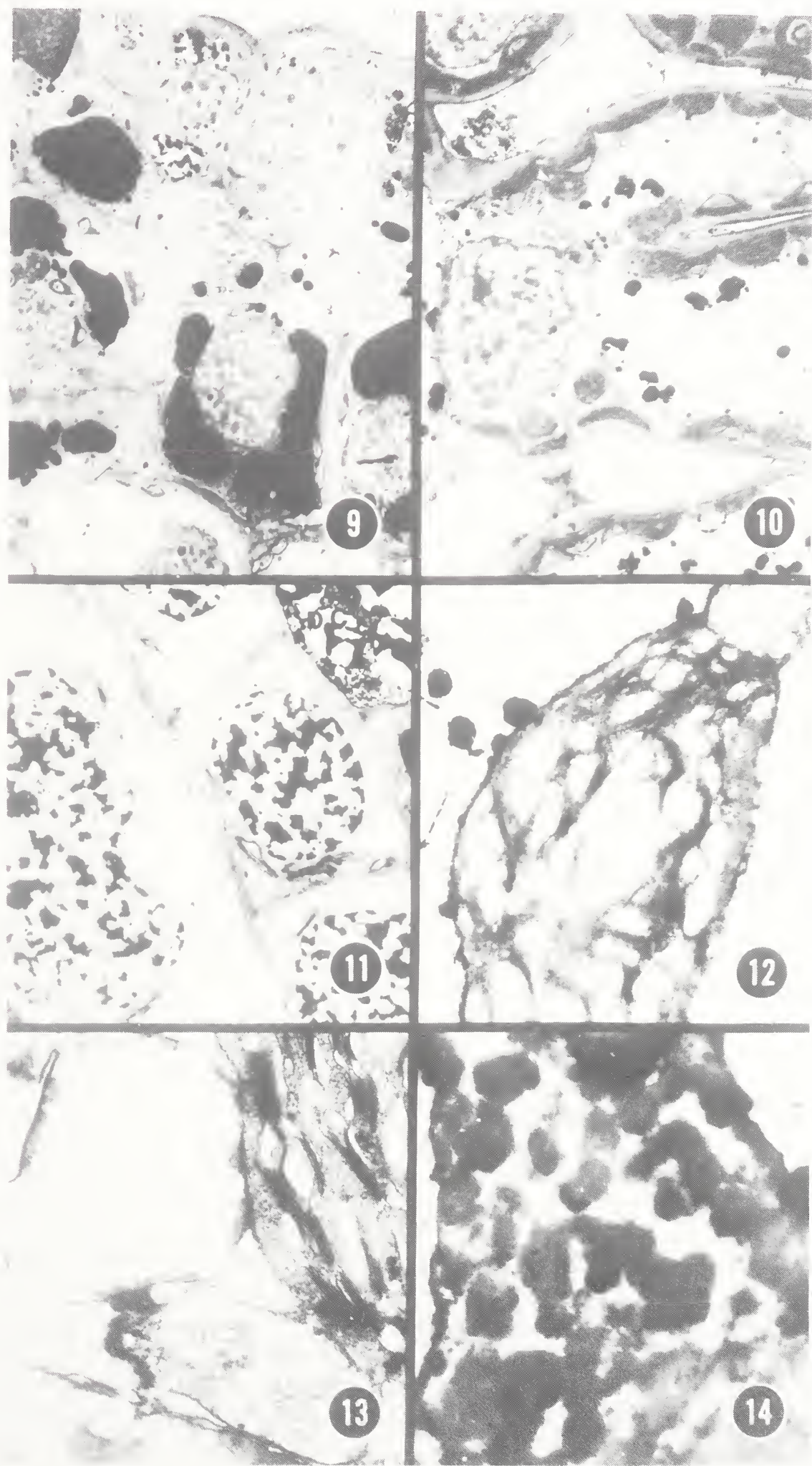
Figures 3-8 show the views of *P. strobus* control needles imaged with transmission electron microscopy. Stage 1 degradation was often unchanged as indicated in the text.

- Figure 3.** Low magnification view of the basal portion of a first year *P. strobus* needle in transverse section. Epidermal and hypodermal layers lie outside of the plicate mesophyll cells. Large deposits of tannins (T) fill the central vacuolar regions of the cells. Chloroplasts can be observed to contain large starch deposits. 15,300 X.
- Figure 4.** Nucleus from mesophyll cell in the tip region. Note the invaginations and the random distribution of eu- and heterochromatins. Prominent starch and plastoglobuli can be seen in the surrounding chloroplasts. 5,000 X.
- Figure 5.** Meristematic zone at the base of needle. Cells possess large, prominent nuclei. Ch = metaphase chromosomes. 15,000 X.
- Figure 6.** Chloroplast with adjacent mitochondria and peroxisome from mesophyll cell in tip region of pine needle. Free ribosomes are in the cytoplasmic matrix. Variable thylakoid numbers comprise the chloroplast grana. The chloroplast stroma is more dense relative to mitochondrial and peroxisome matrices. Note the prominent dark plastoglobuli often appearing in clusters (Pg). 19,400 X.
- Figure 7.** Portion of nucleus and chloroplasts in control tip. Note the deep invagination of the nuclear envelope (arrow). 20,500 X.
- Figure 8.** Nucleolus from nucleus in a control tip mesophyll cell. Both granular (G) and fibrillar (F) components are present, as well as cleared areas referred to as nucleolar vacuoles (NV). 30,000 X.



Figures 9-14 show the views of *P. strobus* SO₂-fumigated needles imaged with the transmission electron microscope. Views represent examples of stages 2 and 3 from random degradation among mesophyll cells in all regions of the developing needles.

- Figure 9.** Low magnification view of the basal portion of a first year *P. strobus* needle in transverse section close to the meristematic zone. Tannin deposits are extensive. Chloroplasts contain starch, although in reduced quantity, compared with control. 1,500 X.
- Figure 10.** Tip region (5 days fumigation) showing partial breakdown of the cytoplasm and a clearing of the euchromatin in the nuclei. Starch in chloroplasts is more sparse than in the control cells. 1,400 X.
- Figure 11.** Portion of meristematic zone in the basal region of a needle from an SO₂-treated plant. Eu- and heterochromatin appear normal. Occasional degraded cells (DC) appear in normal development. Compare with Fig. 5. 4,500 X.
- Figure 12.** Portion of chloroplast and mitochondrion representative of stage 2 degradation. Stroma of chloroplast is more dense than unaffected material, but matrix of mitochondrion has become nearly translucent. Significant thylakoid swelling can be observed in the chloroplast. 16,600 X.
- Figure 13.** Stage 3 degraded chloroplast from tip cell following five days fumigation. The starch remains, but the stroma and thylakoid membranes are beginning to form a dense mass. 25,000 X.
- Figure 14.** Stage 3 degradation of nucleus from SO₂-affected mesophyll of needle tip region. The heterochromatin is coagulated into a reticulum showing a "fuzzy" appearance prior to the complete destruction of the organelle. 20,000 X.



The Impact of Sulfur Dioxide Fumigation on the Ultrastructure and Photosynthesis of Pine Needles

II. Resin Duct Epithelial Cells

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Abstract

Ultrastructural observations of epithelial cells from resin ducts in the expanding needles of *Pinus strobus* seedlings were made from control and from green portions of SO₂-fumigated seedlings. Three needle zones were selected: the basal region (enveloped within the fascicular sheath), mid-region, and tip. In SO₂-fumigated material, the ultrastructural appearance of the epithelial cells was found to vary greatly with the position of the cells and the length of fumigation treatment. No visible change in ultrastructure was observed in epithelial cells taken from the basal region of needles after short fumigation, but after longer SO₂-treatment, no normal epithelial cells were found. In the middle needle portion, most samples contained normal epithelial cells, but after longer treatment, there were signs of premature senescence. In the oldest portions of the needle (the tip), some samples contained normal epithelial cells but most of the cells exhibited pronounced, but reversible signs of degeneration.

Introduction

Only a few studies on the impact of sulfur dioxide on the structure of pine needle tissues other than mesophyll have been conducted. This is particularly the case with the epithelial cells of resin ducts. Based on only light microscope observations, previous studies showed that the epithelial cells underwent severe hypertrophy resulting in the complete occlusion of the resin duct canals after a 3-hour exposure to 1.0 ppm SO₂ (Smith and Davis, 1978; Stewart *et al.*, 1973). Such reported change was evident not only in the portion of the needle that displayed macroscopic symptoms but, unlike other tissues, extended far into the apparently healthy regions. Microscopic injury was observed only in growing needles which exhibited macroscopic damage, such as a tan necrosis extending from the needle tip toward the base. Necrotic areas were separated from uninjured green ones by an abrupt line of demarcation, a so-called "transition zone" (Smith and Davis, 1978). However, according to Evans and Miller (1975) in *P. pon-*

derosa, SO₂ fumigation caused a loss of cellular constituents and cell wall material from epithelial cells. In most cases, only cell walls and a small amount of the cytoplasm remained in injured epithelial cells after 9 days of SO₂ exposure (0.45 ppm). Our study was initiated in order to determine the effects of SO₂ exposure on the ultrastructure of epithelial cells from resin ducts in elongating *Pinus strobus* needles.

Materials and Methods

Three year-old *Pinus strobus* seedlings were exposed to 0.8 ppm of sulfur dioxide (SO₂) for 4 hours daily over a period of either five or nine days, respectively. No microscopic symptoms of SO₂-induced injury on the elongating needles were observed after 5 days treatment, but after 9 days, at the conclusion of the experiment, visible damage appeared as small chlorotic spots on the needles. Epithelial cells in only green, and apparently healthy needle portions of potted seedlings previously maintained under greenhouse conditions, were studied.

At the conclusion of either fumigation period, one mm needle segments were excised and fixed in phosphate-buffered osmium tetroxide. After ethanolic dehydration and infiltration with propylene oxide, the specimens from fumigated material and controls were infiltrated and subsequently embedded in a 1:1 Spurr-Epon epoxy mixture. Specimens were cut into ultrathin sections, stained with lead citrate, and observed with a Hitachi H-600 transmission electron microscope operating at 75 kV. Comparative observations were made at corresponding magnifications.

Results

The resin ducts in pine needles are dual elongated structures extending beneath the longitudinal axis of the adaxial needle surface (Fig. 1). They are composed of one layer of thin-walled, small, elongated epithelial cells surrounding a lumen, or canal, where resin is

accumulated.

The epithelial cells of *Pinus* resin ducts display a characteristic fine structure which is related to the specialization and concentration of organelles involved in oleoresin synthesis (Fahn, 1979; Vassilyev, 1977). The cells differentiate very closely to the basal meristematic region of the needle which gives rise to all of the leaf cells. The epithelial cells become fully mature and elongated while they are still enclosed within the fascicular sheath. The rate of resin synthesis and the amount of secretion gradually diminish in the acropetal direction.

The most notable feature of the epithelial cells are the leucoplasts which, in the highly active portion of the duct, occupy a very large part of the cytoplasmic volume (Fig 1). The leucoplasts usually have no internal membranes and their stroma lack ribosomes. Characteristic of these epithelial leucoplasts is their specific connection to the endoplasmic reticulum (ER), the cisterna of which completely surrounds the plastid envelope. The periplastidal reticulum (or reticular sheath) is continuous with well-developed agranular and granular cytoplasmic profiles of the ER extending throughout the cell, and approaching the mitochondria and plasmalemma. Synthesis of resin occurs not inside the matrix of organelles and in cytosol, but separately within the intermembranous spaces of the plastid, nuclear and mitochondrial envelopes, and is presumably transported to the periplasmic space through the ER which is also involved in resin synthesis. Resin is eliminated from periplasmic spaces into the canal through the thin, loose apical cell wall. In epithelial cells of the youngest portion of the needle, there are smaller and less frequent leucoplasts only partly sheathed by a periplastidal reticulum, and the number of resin droplets is sparse.

In the epithelial cells in which resin synthesis has slowed, the amount of intracellular resin is also reduced as are the number and size of the leucoplasts. The resin completely disap-

pears from the nuclear envelope; however, the reticular sheath is still complete. The cell wall becomes thickened and dense. In the tip region of *P. strobus* needles, the epithelial cells remain intact but quiescent, and the ER sheath around lipids show large gaps at certain sites.

In SO₂-treated material, the ultrastructural appearance of epithelial cells varies greatly with the position of the cells and the mode of treatment. We could not find changes in the ultrastructure of the epithelial cells from the basal parts of the growing needles when the plants were fumigated for 5 days, even when the mesophyll cells in some parts of the needle displayed severe damage. The fully-active epithelial cells were dominated by leucoplasts which were completely enveloped by the ER cisterna. They also contained abundant free ribosomes. However, there were no osmophilic substances inside the intermembranous spaces of organelles (Fig. 2).

In some samples of 5-day treated specimens, the epithelial cells of the oldest portion of the needle, the tip, appeared less functional and contained leucoplasts and resin droplets within the intermembranous space of the organelles. In some samples, however, there were pronounced signs of degeneration. The epithelial cells were highly vacuolated and flattened in radial directions, but the nucleus appeared normal. The number of leucoplasts and other organelles was significantly reduced and there were no reticular sheaths. The epithelial cells contained large lipid bodies characteristic of inactive cells. The remaining organelles were ill-defined. In some samples, there was an aggregation of vesicles containing several dense granules. The apical cell wall facing the canal became dense and thickened and the plasmalemma was retracted from the cell wall. No hypertrophy of the epithelial cells was found, although they showed slight plasmolysis. The lumen of the canal was completely open.

After longer SO₂ treatment (4 hr/day dur-

ing 9 days), no normal epithelial cells were found within the youngest portion of the needle protected by cataphylls of the fascicular sheath. The ultrastructure of such epithelial cells showed severe damage. The integrity of the leucoplast and mitochondrial envelopes as well as the reticular sheath was lost and the plastid stroma became flocculent amid small membrane fragments (Fig. 3). Resin droplets were still present and, unlike control plastids, osmophilic material was precipitated within the stroma of some leucoplasts. In the most severe damage, only membrane fragments remained of the plastids and periplasmic membranes with no evidence of resin. Occasional starch grains could be found (Fig. 4).

In spite of the above plastid changes, the mitochondrial nucleoids with DNA fibrils appeared intact. The cytosol became empty and the ribosomes were ill-defined. The tonoplast was broken down and the double outer membranes of the mitochondria were often indistinguishable. Nevertheless, the Golgi apparatus and the nucleus appeared normal and the plasmalemma was tightly appressed to the cell wall. No hypertrophy or collapse of the epithelial cells described in earlier light optical studies were noted.

In mid-region needle specimens, it was found that the periplastidal endoplasmic reticulum disappeared completely (Fig. 5) and the number of cytoplasmic reticular profiles was significantly reduced. No osmophilic resin droplets were seen. Within the normally appearing nuclei, the nucleoli of such epithelial cells were almost devoid of the granular component (which would indicate an inactive state), and their size was smaller than in the nuclei of the adjacent mesophyll cells where the proportion of the granular component was much higher (more active nucleoli). There was great variation in the physical state of mesophyll cells within the vicinity of injured resin ducts. In some samples, the mesophyll cells appeared relatively normal, but in some cases, they were

severely injured, showing the loss of membrane integrity of the chloroplasts.

Discussion

There were two distinct types of epithelial cell injury due to SO₂-treatment. First, there was a disappearance of the ER sheath around the leucoplasts, reduction in organelle frequency, and disappearance of resin droplets from protoplasts. The integrity of organelles and membranes was not lost. It follows that, unlike mesophyll chloroplasts which are affected first (Huttunen and Soikkeli, 1984; Stewart *et al.*, 1973), leucoplasts of the epithelia are less sensitive to SO₂ treatment than the ER. This type of reversible injury (similar to premature senescence) was observed only in the epithelial cells of the needle tip region after milder treatment, whereas the cells in younger (mid- and basal-needle regions) remained unchanged. The apical portion of the needle eventually died even after mild treatment. After longer SO₂-exposure, a similar type of alteration was observed in the epithelial cells of middle regions of some needles where the epidermal cells deposited thick secondary walls while cells in basal portions of the needle underwent irreversible changes.

Secondly, the loss of organelle integrity (leucoplast and mitochondria) and membrane integrity (endoplasmic reticulum and tonoplast), along with the disappearance of ribosomes were found, but with no apparent changes in Golgi-apparatus, nucleus and plasmalemma. The resin droplets remained in surrounding degenerating cytoplasm. It follows that, in the epithelial cells, the nucleus, plasmalemma and Golgi-apparatus are most resistant as opposed to the situation with mesophyll cells, and the sheathing ER is most sensitive to the SO₂ treatment. Unlike mesophyll chloroplasts, leucoplasts of the epithelial cells are less sensitive to SO₂ pollution than the endoplasmic reticulum.

The two different types of ultrastructural

alteration are not different stages of the same process leading to death of the epithelial cells. Unlike mesophyll cells (Kravkina *et al.*, 1989), epithelial cells are most sensitive to longer SO₂ treatment in the basal region of the growing needle where they are most active in resin production, and where the epidermal cells have thin, non-cutinized cell walls, which lacking epicuticular wax, is readily susceptible to injury from toxic gases. In this needle region, the longer SO₂-treatment leads to irreversible ultrastructural changes of the epithelium. However, with shorter treatment (5 days), the epithelial cells in the basal portion remained unchanged. It follows that the pattern of change depends on pollutant exposure. In shorter treatment, epithelial cells of the tip region are sensitive, and in the other regions they are resistant; however, in longer treatment, all parts of the needle appear affected. In the basal parts of the needle, the changes are irreversible, while in the middle part they are reversible. Unlike the mesophyll, where the cells at different stages of degradation were randomly distributed within the tissue (Kravkina *et al.*, 1989), all the epithelial cells have similar ultrastructure at a given axis level of the SO₂-treated needle. Likewise, the response of organelles, especially nucleus and mitochondria of the epithelial cells, to SO₂-treatment differs distinctly from that of mesophyll cells. The results of our study differ significantly from those of previous light microscope observations (Smith and Davis, 1978; Stewart *et al.*, 1973) in which hypertrophy of the epithelial cells leading to the occlusion of the resin duct after SO₂-treatment was found. The possible explanation for the discrepancy is that the previous investigators studied mature needles of *P. sylvestris* and *P. strobus*. Evans and Miller (1975), who studied the anatomy of SO₂-fumigated developing needles in *P. ponderosa*, also did not reveal hypertrophy of the epithelial cells. Thus, SO₂ fumigation not only results in the reduction of the rate of photosynthesis (Kravkina *et al.*, 1989), but also adversely affects oleoresin synthesis. These results should be taken into account in evaluations of the

environmental impact related to SO₂ emissions.

Acknowledgments

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Literature Cited

- Evans, L.S., and P.R. Miller. 1975. Histological comparison of single and additive ozone and sulphur dioxide injuries to elongating ponderosa pine needles. *Am. J. Bot.* 62:416-421.
- Fahn, A. 1979. *Secretory Tissues in Plants*. Acad. Press, London, New York.
- Huttunen, S., and S. Soikkeli. 1984. Effects of various gaseous pollutants on plant cell ultrastructure. In: *Gaseous Air Pollutants and Plant Metabolism*. Koziol and Whatley (eds). pp. 117-127.
- Kravkina, I. M., E. A. Miroslavov and R. E. Crang. 1989. The impact of sulfur dioxide fumigation on the ultrastructure and photosynthesis of pine needles. I. Mesophyll cells. In: *EPA/USDA 2nd Int. Symp. on Air Pollution Effects on Vegetation*. (Raleigh, NC).
- Smith, H.J. and D.D. Davis. 1978. Histological changes induced in Scotch pine needles by sulfur dioxide. *Phytopathology* 68:1711-1716.
- Stewart, D., M. Treshow and F. M. Haznez. 1973. Pathological anatomy of conifer needle necrosis. *Can. J. Bot.* 51:983-988.
- Sutinen, S. 1987. Ultrastructure of mesophyll cells of spruce needles exposed to O₃ alone and together with SO₂. *Eur. J. Forest Pathol.* 17:362-368.
- Vassilyev, A.E. 1977. *Functional Morphology of Plant Secretory Cells*. Nauka Publ. House, Leningrad (in Russian).

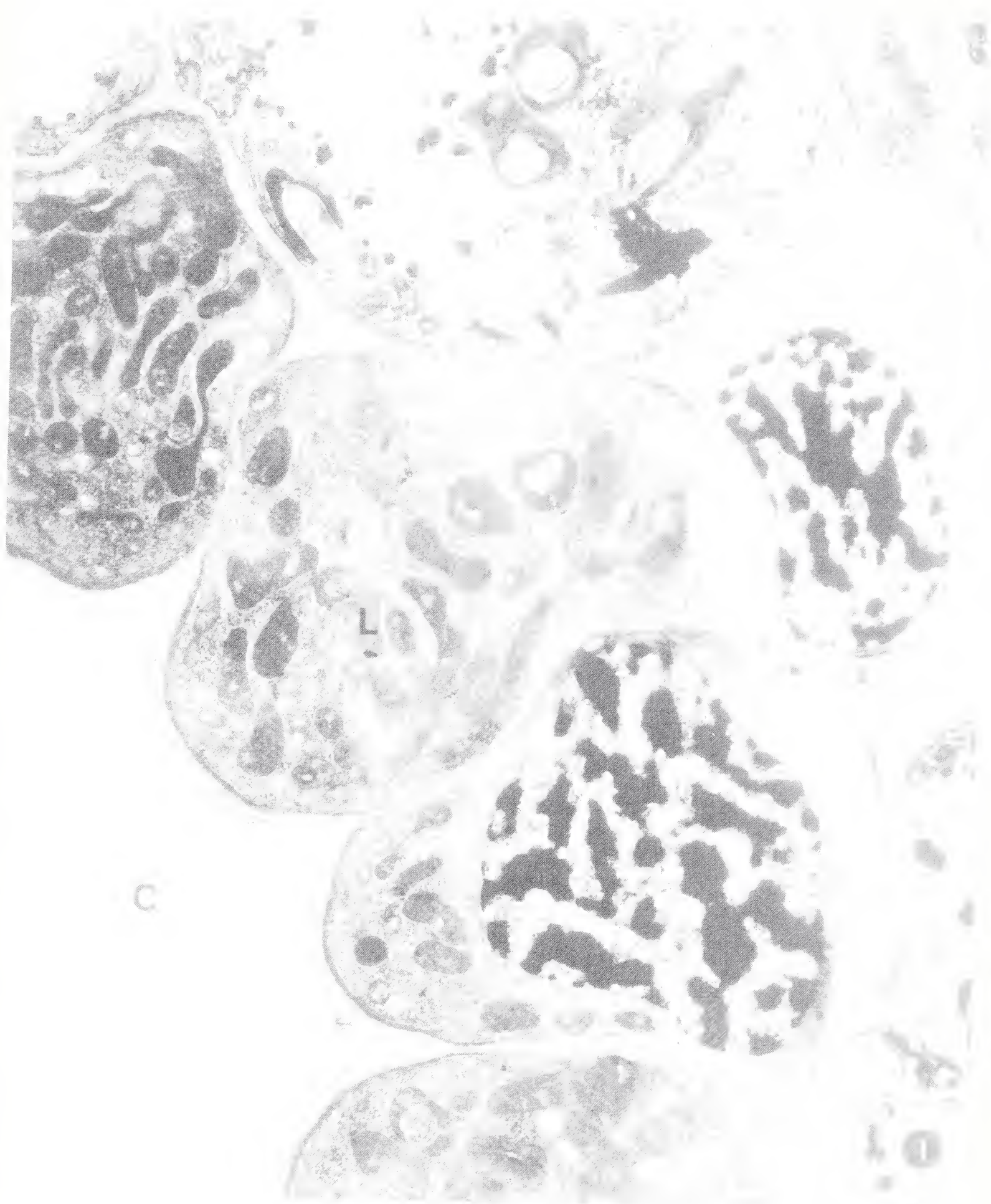


Figure 1. Epithelial cell of the basal region of the *Pinus strobus* needle after short (0.8 ppm, 5 days, 2 hr) SO₂-treatment. Appearance is similar to control. Note the normal appearance of all organelles, but the lack of resin droplets in the extra-cytoplasmic phase of the protoplast. L=leucoplasts, C=canal. 3,500X.

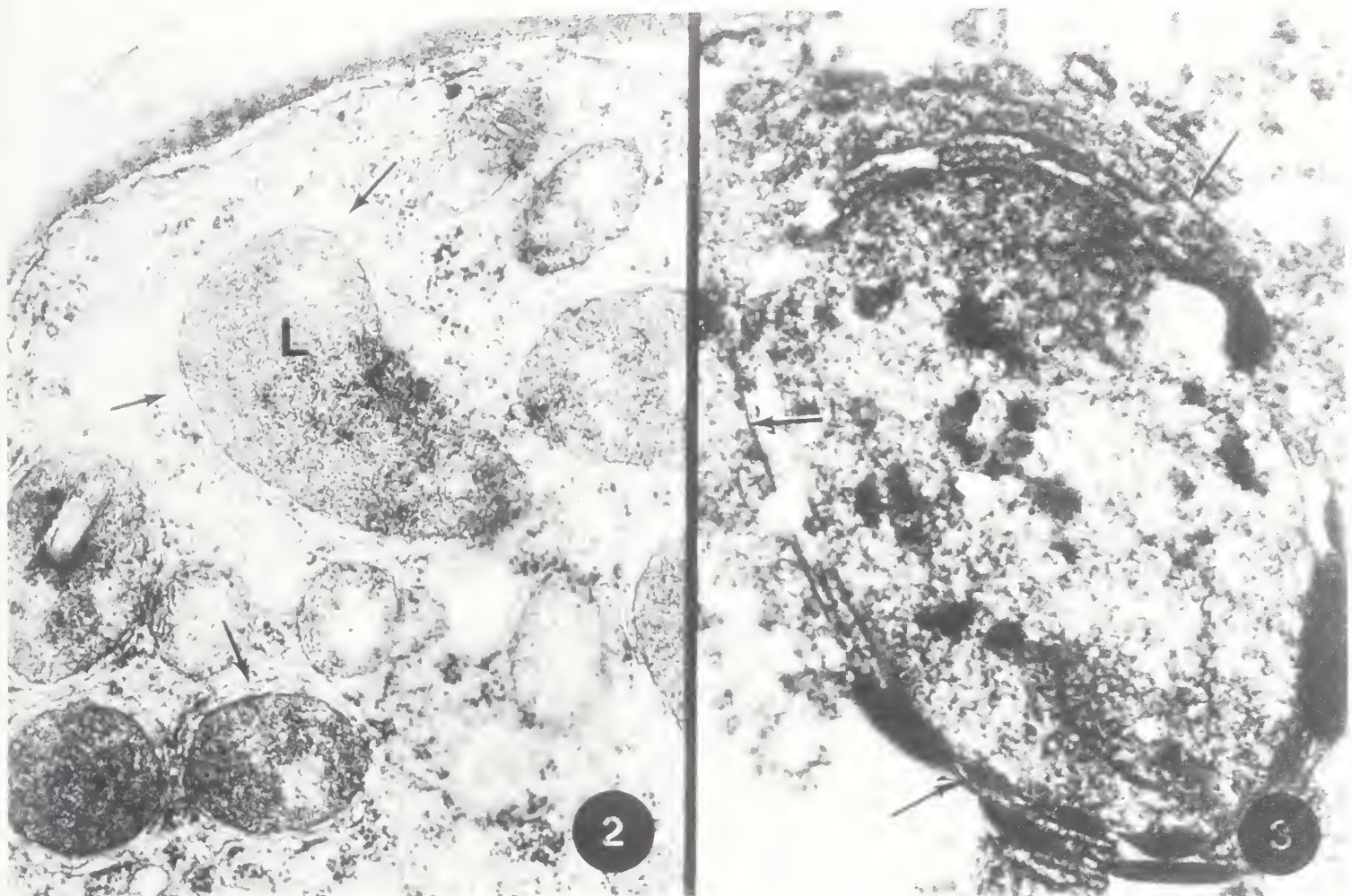


Figure 2. Portion of an epithelial cell at the base of the needle after long SO_2 -treatment. Note the lack of resin, the sheath of ER (arrows) around leucoplasts (L), and the normal appearance of organelles. 20,000X.

Figure 3. A portion of the epithelial cell in the basal region of the needle after long (0.8 ppm, 9 days, 4 hr.) SO_2 -treatment. Note the loss of the integrity of the Leucoplast, and sheathing ER membranes (thin arrows), and the flocculation of stroma (white arrow). 30,000X.

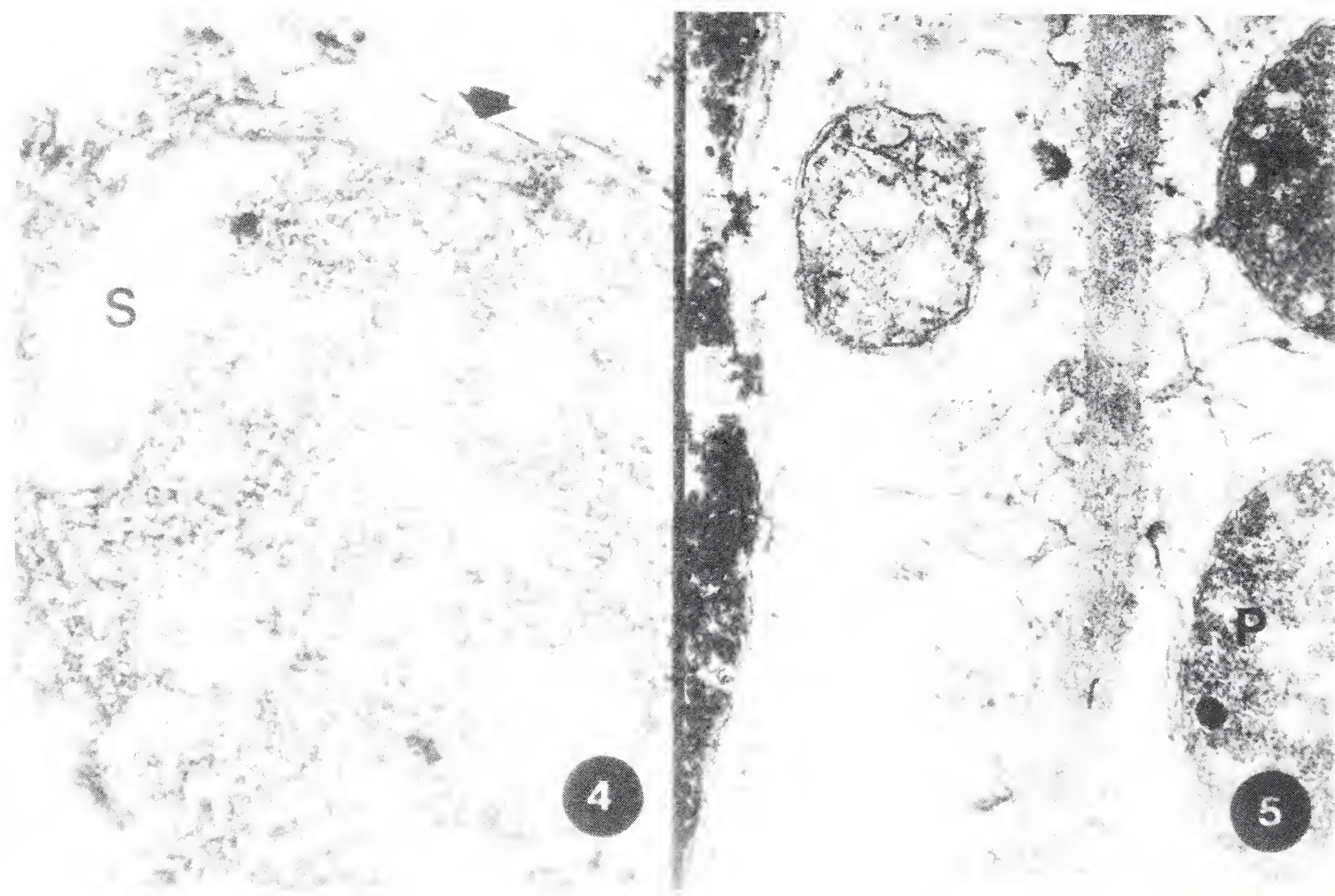


Figure 4. Severe damage to plastid induced by strong SO_2 treatment. Resin is lost but a starch grain (S) remains. 30,000X.

Figure 5. Mid-region needle specimen showing loss of periplastidal endoplasmic reticulum. P=plastid. 30,000X.

The Impact of Sulfur Dioxide Fumigation on Photosynthetic and Ultrastructural Responses of Mesophyll Cells in Developing *Pinus strobus* Needles. III. Transition Zone.

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Abstract

Three year-old eastern white pine (*Pinus strobus*) seedlings were fumigated with sulfur dioxide (SO₂) for 4 hours daily for 9 days during the time of new needle emergence at levels of 0.5, 0.8 and >1.0 ppm. Low-level damage appeared as chlorotic mottled regions in distal needle portions. Higher level fumigation resulted in complete necrosis of the needles which progressed basipetally. The transition between the necrotic brown and the living green tissues was abrupt. However, no detectable surface differences were noted, the damage being confined to subepidermal tissues. Distinct differences were observed in the elemental composition of affected needles on opposite sides of the transition zone.

Introduction

The alteration of foliar structure due to air pollution damage generally appears visibly as lesions, mottling, or as widespread progressive chlorosis and necrosis. Such visible changes often belie the sudden and drastic changes

observed in mesophyll tissues at the microscopical level (Kravkina *et al.*, 1989; Maurice and Crang, 1989; Crang and McQuattie, 1987). While few observations have been made at the cellular and subcellular level of air pollutant-induced damage, even fewer have been recorded of damage effects in gymnosperms. Most of these have concentrated solely on chloroplast responses within foliar tissues, or on epicuticular wax deposits at the foliar surface (e.g. Sutinen, 1986; Huttenen and Laine, 1983). It is our intent to couple microscopy and analytical techniques in order to document the transition gradient from healthy to damaged first year foliar structures in *Pinus strobus* as affected by sulfur dioxide exposure.

Materials and Methods

Three year-old potted *Pinus strobus* seedlings were fumigated with sulfur dioxide (SO₂) at concentrations of 0.5, 0.8 and approx. 1.5 ppm for 4 hours daily over a 9 day period. Fumigation was conducted in light-transparent CSTR chambers under greenhouse conditions. Ambient conditions served as the control.

Needles from first year growth were removed from plants at the conclusion of the fumigation schedule and were air-dried (48 hr) for scanning electron microscopy (SEM) and energy-dispersive x-ray microanalysis (EDX), or fixed and embedded for transmission electron microscopy (TEM) as outlined by Kravkina *et al.* (1989). 1-2 μm thick sections were obtained for light microscopy (LM) and were stained with 1% aqueous toluidine blue for 30 seconds. Ultrathin sections for TEM were obtained from regions of embedded specimens which were first observed by LM. The transition zone observed visually was identified in SEM preparations by a corresponding mark on the supporting mount adjacent to the needles.

Results and Discussion

At SO_2 concentrations of 0.5 and 0.8 ppm, needle tip burn and chlorotic mottling in the distal portions were evident at the conclusion of the experiment. However, when the level of SO_2 exceeded 1.0 ppm, a progressive necrosis extended basipetally, with a sharp line of demarcation between it and green (apparently healthy) needle regions (Fig. 1). Examination of needles showing this distinct transition zone was made with the aid of the SEM, and revealed no evident structural disturbance of the surface waxes, epidermal integrity, or stomatal appearance (Fig. 2). This indicated that all affected tissues were subepidermal, and that the route of entry of SO_2 was through normal channels (i.e. stomata), and not through disruptions of the needle surface (Danilova *et al.*, 1987).

Needle segments taken from the transition zone were examined both by TEM (Figs. 3,4) and by LM (Fig. 5). In most cases, the transition from healthy to severely damaged mesophyll cells was sudden, with adjacent cells showing dramatic differences in ultrastructural appearance. Figures 3 and 4 show chloroplasts from adjacent cells in which the healthy-appearing plastid (Fig. 3) was seemingly identical to those from control specimens (ambient air

conditions). The damaged plastids revealed swelling and loss of substance within the stroma. The thylakoid membranes were distended to the point of disruption, but plastoglobuli persisted (Fig. 4). While starch grains were sometimes found in the affected cells, their frequency was less than in plastids on the green side of the transition zone.

This distinct demarcation within the mesophyll was documented in longitudinal sections taken at the site of the transition zone and viewed with LM (Fig. 5). Damaged cells were collapsed and revealed a loss of most protoplasmic substance. Details of the damage were identical to those described by Kravkina *et al.* (1989) with the exception that an even more sudden change was induced by the higher concentration of SO_2 and the longer fumigation schedule.

Elemental determinations made by means of EDX typically showed high levels of potassium (K) on the green side of the transition zone (Fig. 6) with lesser emissions for silicon (Si), chlorine (Cl) and calcium (Ca). Virtually identical spectra were obtained from control specimens. Presumably, Cl was complexed with K and in organic molecules, while Si and Ca represented important elements in the cell wall composition. Adjacent needle segments from the brown (damaged) side of the transition zone showed these same elements (with the exception of Cl), but also with significant quantities of magnesium (Mg), phosphorus (P) and sulfur (S) present (Fig. 7). In all cases, the peak-to-background ratios of the elements were greater than those in spectra obtained from the green portions of needles. This may be due to the greater desiccation in the brown region and would explain why the background emission levels were higher in the green regions (i.e. greater residual water contributing to greater mass).

It is entirely possible that Mg, P and S are natural components of the needle tissues, but which were not observed in the green regions

because they simply were not sufficiently concentrated for EDX detection. While it is tempting to state that the presence of S in the brown regions is due to binding of that element from the SO₂ fumigation, it cannot be conclusively determined by these experimental procedures. However, S peaks in fully-desiccated control needles were only barely perceptible and did not possess peak-to-background ratios higher than 1.2, a value generally not considered to be significant. No explanation can be given for the lack of Cl in the brown needle regions.

This study reveals that the transition of foliar damage in *P. strobus* needles is related to the SO₂ dose levels and, at the higher concentration, surface structure is unaffected but mesophyll collapse is sudden, resulting in extensive cytoplasmic damage and a distinctive change in the pattern of elements detectable by EDX. The correlation of these results is conclusive. Of particular interest was the recovery of plants almost completely damaged by fumigation with >1.0 ppm SO₂. New, normal-appearing needles were found to emerge later in the same growing season, indicating that the new growth and meristematic activities were not permanently damaged.

Acknowledgments

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Literature Cited

- Kravkina, I.M., E.A. Miroslavov, and R.E. Crang. 1989. The impact of sulfur dioxide fumigation on the ultrastructure and photosynthesis of pine needles. I. Mesophyll cells. In: *EPA/USDA 2nd Int. Symp. on Air Pollution Effects on Vegetation*. (Raleigh, NC).
- Maurice, C.G., and R. E. Crang. 1989. Foliar injury and shoot growth in response to prolonged acidic misting of *Pinus strobus* seedlings. *Arch. Environ. Contam. Toxicol.* 18:277-284.
- Crang, R.E., and C.J. McQuattie. 1987. A quantitative light microscopic technique to assess the impact of air pollutants on foliar structure. *Trans. Am. Microsc. Soc.* 106:164-172.
- Sutinen, S. 1986. Ultrastructure of mesophyll cells in and near necrotic spots on otherwise green needles of Norway spruce. *Europ. J. Forest Path.* 16:379-384.
- Huttenen, S., and K. Laine. 1983. Effects of air-borne pollutants on the surface wax structure of *Pinus sylvestris* needles. *Ann. Bot. Fennici* 20:79-86.
- Danilova, M.F., I.M. Kravkina, R. E. Crang, and D. Pechak. 1987. Ultrastructure of stomata and leaf surface in *Populus deltoides* (Salicaceae) under SO₂ influence. *Bot. J. USSR Acad. Sci.* 72:1187-1194.

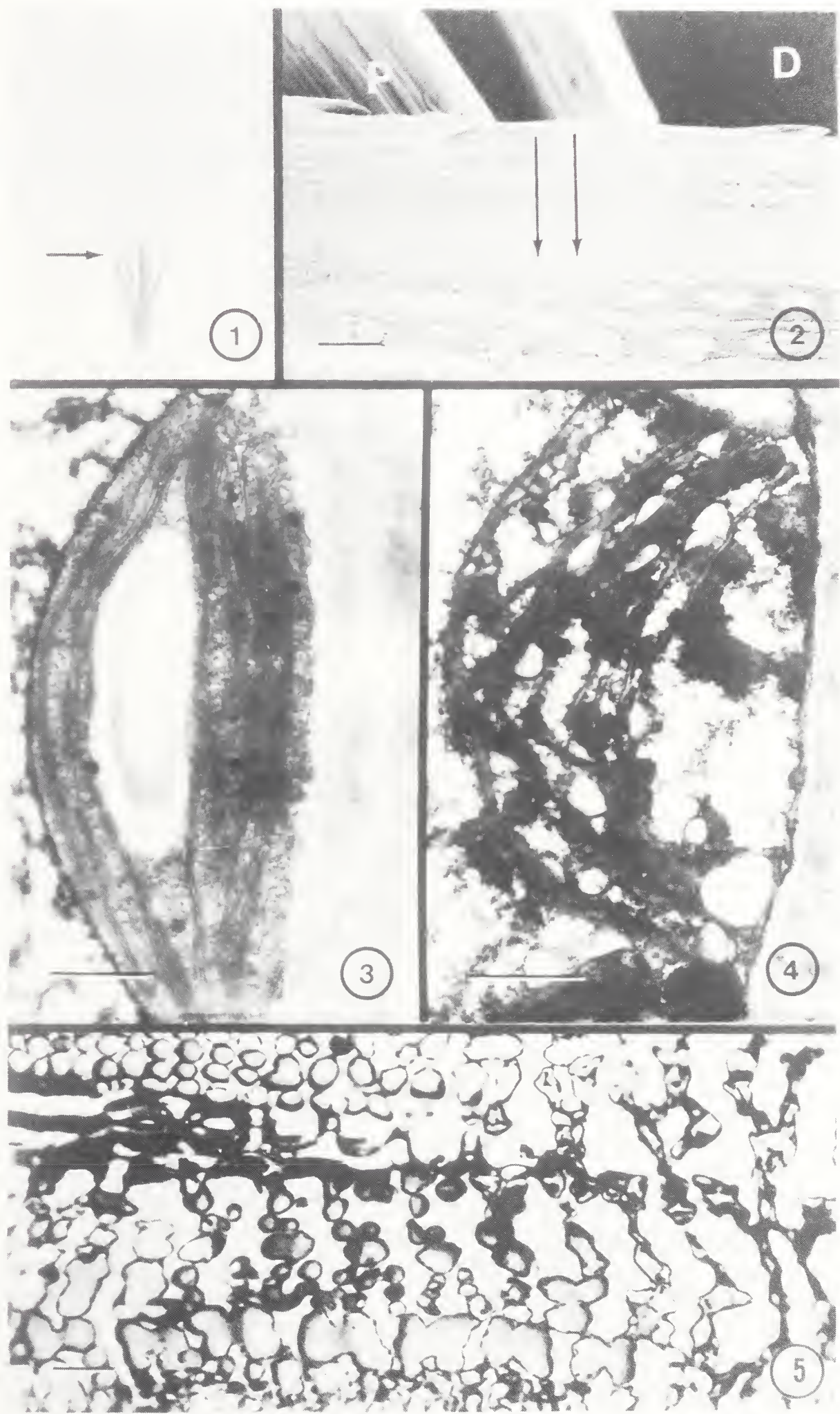
Figure 1. Macroscopic view of first year needles of *P. strobus* exhibiting abrupt transition zone (arrow) above fascicular sheath.

Figure 2. Scanning electron microscopic view of transition zone in which no observable surface damage can be found in either proximal (P) or distal (D) regions adjacent to the sudden transition of damage (arrows). Bar = 0.1 mm.

Figure 3. Normal-appearing plastid in plicate mesophyll cell viewed with transmission electron microscopy Bar = 0.5 μ m.

Figure 4. Highly damaged plastid in adjacent cell to that of Fig. 3. Bar = 0.5 μ m.

Figure 5. Light micrograph of longitudinal section of needle as in above figures showing sudden transition from healthy cells (left) to damaged cells (right). Bar = 0.1 mm.



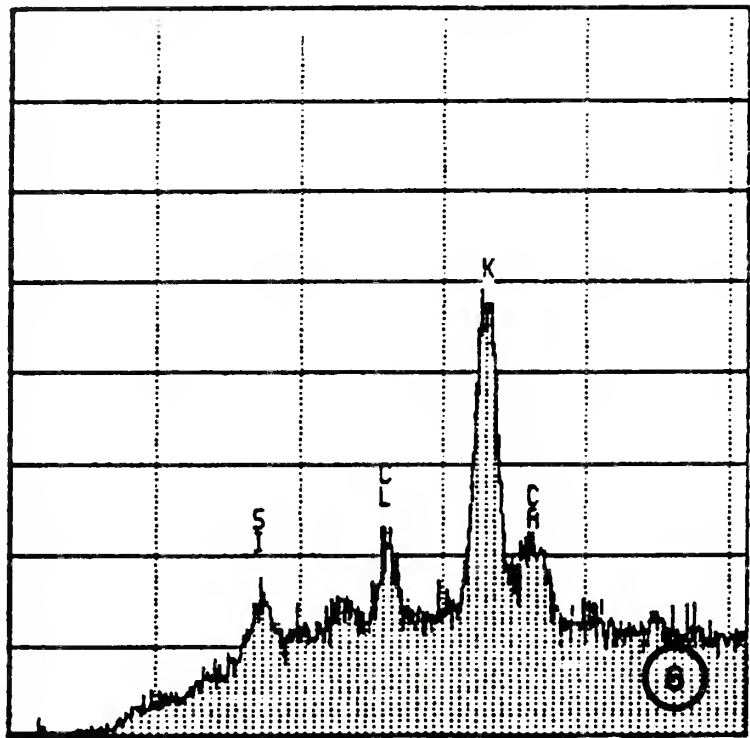


Figure 6. EDX spectrum of elements found on green portions of SO₂-fumigated needle. Element peaks are (left to right): Si, Cl, K and Ca.

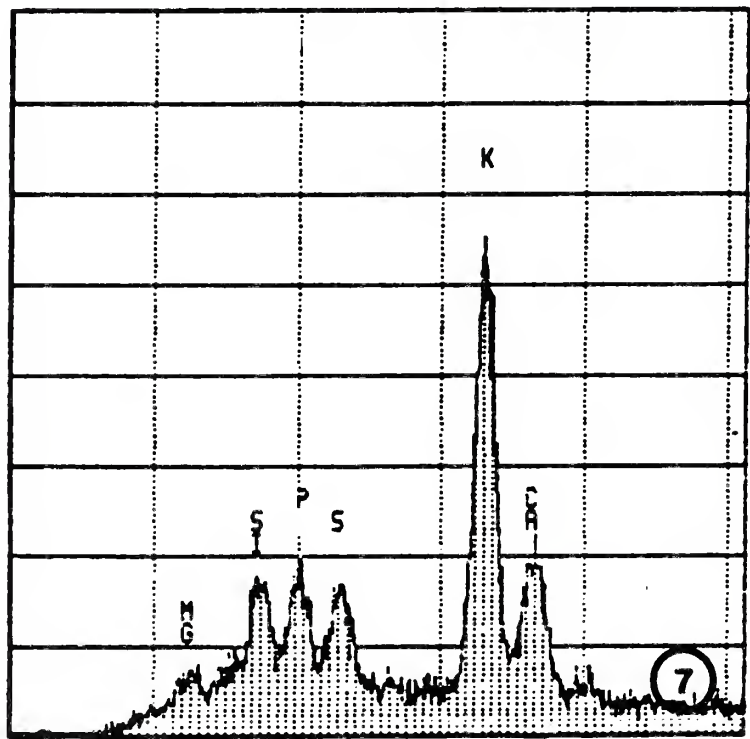


Figure 7. EDX spectrum of elements found on brown (necrotic) portions of SO₂-fumigated needle. Spectrum is from same needle as in Figure 6. Elements (from left to right) are: Mg, Si, P, S, K and Ca. Scale is same as in figure 6.

Ozone Concentration in Leaf Intercellulars is close to Zero

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Abstract

Transpiration and ozone uptake rates were measured simultaneously in sunflower leaves at different stomatal openings and ambient ozone concentrations. Ozone uptake rates were proportional to the ozone concentration up to 1500 ppb. The leaf gas phase (stomatal plus boundary layer) resistance for water vapor r_{gw} was calculated and converted to the resistance for ozone r_{gz} multiplying it by the theoretical ratio of diffusion coefficients for water vapor and ozone in air (1.67). The ozone concentration in intercellulars calculated from the ozone uptake rate and r_{gz} scattered around zero. The ozone concentration in intercellulars was measured directly by supplying ozone to the leaf from one side and measuring the equilibrium concentration above the other side, and it was found to be zero. The total leaf resistance for ozone was proportional to the gas phase resistance for water vapor with a coefficient of 1.68.

It is concluded that ozone enters the leaf by diffusion through stomata, and it is rapidly

decomposed in cell walls and the plasmalemma region.

Plants are sensitive to atmospheric ozone which causes the reduction of their growth rate (Kress and Skelly, 1982; Miller *et al.*, 1982). Photosynthesis was reported to be reduced by the presence of ozone before the symptoms of damage were visible in leaves (Lehnherr *et al.*, 1987). In Scotch pines, the ozone uptake rate was closely correlated with transpiration, suggesting that the main route of ozone into the leaf was through stomata (Skarby *et al.*, 1987). These data suggest that stomata is the main, if not the only route, of entering ozone into leaf intercellulars (Heath, 1980). Obviously, the physical process of ozone transport is diffusion, like it is for water vapor and CO_2 , and this makes it possible to calculate the actual concentration of ozone in leaf intercellulars.

Theory

The method of calculating the intercellular CO_2 concentration is widespread and we applied

the same technique for calculating the inter-cellular O_3 concentration. It is based on the knowledge that in the gas phase of intercellulars, stomatal pores, and leaf boundary layer, the diffusion pathways of CO_2 and water vapor coincide to a great extent. The measurements of the leaf transpiration rate reveal information about the diffusion resistance of the whole gaseous pathway from cell surfaces to ambient air:

$$E = \frac{A_i - A_a}{r_{gw}} \text{ or } r_{gw} = \frac{A_i - A_a}{E} \tag{1}$$

where, E is the transpiration rate (minus cuticular transpiration), r_{gw} , the diffusion resistance in the leaf gaseous phase for water vapor, A_i , the water vapor concentration at evaporating cell surfaces, and A_a , that in the ambient air. Usually we can assume that A_i is close to the saturating water vapor concentration at leaf temperature

$$A_i = A(t_i) \tag{2}$$

where $A(t_i)$ is the saturating water vapor concentration as a function of leaf temperature t_i . CO_2 is a heavier gas ($M_w = 44$) than water vapor ($M_w = 18$), therefore, CO_2 is moving more slowly than water vapor through the same diffusion pathway and at the same concentration differences. The ratio of the diffusion rates of H_2O

and CO_2 in the leaf gaseous pathway was measured to be 1.62 (Oja, 1972).

We could not find a value of the diffusion constant for ozone in air, D_z , in the literature. However, diffusion constants for various gas mixtures may be calculated using the molecular parameters of component gases (Chen and Othmer, 1962).

$$D_{12} = \frac{0.43 \times \left(\frac{T}{100}\right)^{1.81} \times \left(\frac{1}{M_1} + \frac{1}{M_2}\right)^{\frac{1}{2}}}{P \times \left(\frac{T_{k1} \times T_{k2}}{10^4}\right)^{0.1405} \times \left[\left(\frac{V_{k1}}{100}\right)^{0.4} + \left(\frac{V_{k2}}{100}\right)^{0.4}\right]^2} \tag{3}$$

where, M , T , T_k , V_k , P are, correspondingly, molecular weight (g/mol), temperature ($^{\circ}K$), critical temperature ($^{\circ}K$), critical volume (cm³/mol) of a component gas, and atmospheric pressure (bar). Indices 1 and 2 denote component gases. Using values $M_1 = 29$ g/mol, $T_{k1} = 132.3$ $^{\circ}K$ and $V_{k1} = 87.88$ cm³/mol for air (Hodgman and Weast, 1955-56, p. 2121) and $M_2 = 48$ g/mol, $T_{k2} = 260.9$ $^{\circ}K$, $V_{k2} = 147.1$ cm³/mol for ozone (Weast, 1982-83, p. F65) we get at $p = 1$ bar and $T = 298$ $^{\circ}K$ a value of $D_z = 0.137$ cm²/s. Inserting parameters for water vapor $M_2 = 18$ g/mol, $T_{k2} = 647.1$ $^{\circ}K$, $V_{k2} = 55.56$ cm³/mol (Weast, 1982-83, p.

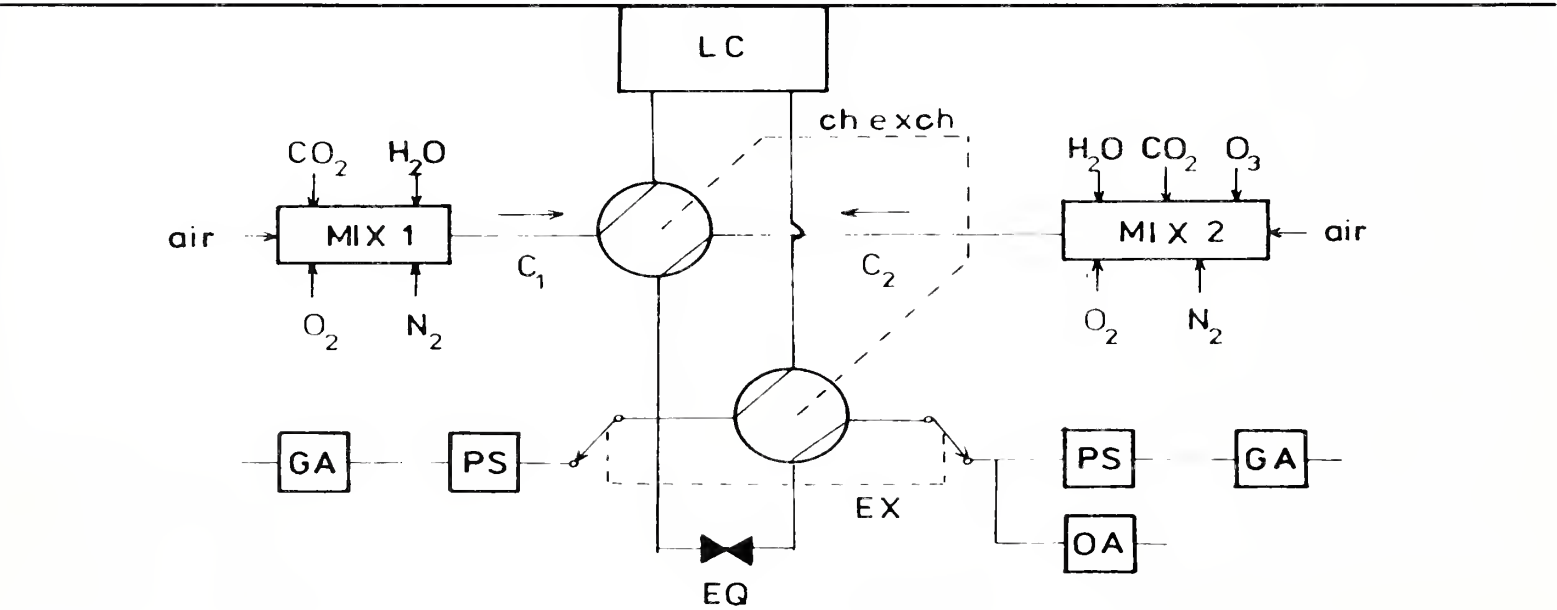


Figure 1. Basic circuit of the two-channel leaf gas chamber exchange measurement system

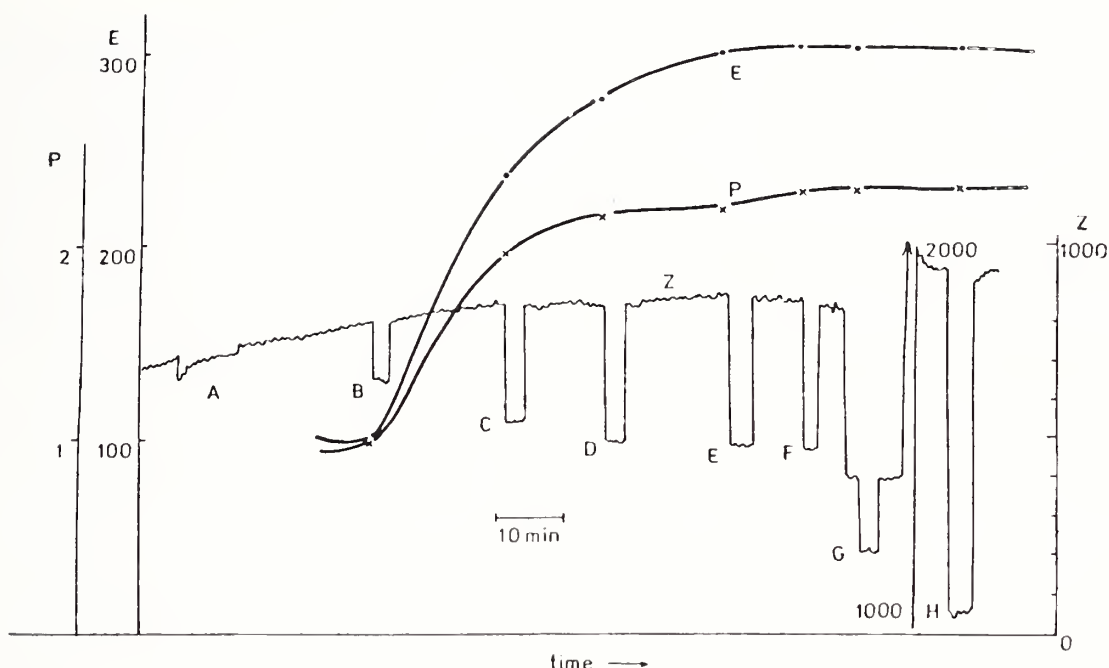


Figure 2. Parallel measurement of photosynthesis, transpiration and ozone uptake in a sunflower leaf

F74) into the same formula yielded $D_w = 0.229 \text{ cm}^2/\text{s}$. Therefore, Eq. (3) gives the ratio of the diffusion coefficients of ozone and water vapor $D_w/D_z = 1.67$. The diffusion resistance for ozone in the leaf gas phase can be calculated as

$$r_{gz} = r_{gw} \times D_w/D_z \quad (4)$$

where r_{gz} and r_{gw} are gas phase resistances for ozone and water vapor, correspondingly, and D_w and D_z are diffusion constants for water vapor and ozone in air. Now it is possible to calculate the ozone concentration in intercellulars from the measured ozone uptake rate:

$$Z_i = Z_a - Q \times r_{gz} \quad (5)$$

where Z is the ozone concentration in ambient (a) and intercellular (i) air, Q is the ozone uptake rate, r_{gz} is from Eq. (4). The ozone uptake rate Q is measured as

$$Q = \frac{(Z_1 - Z_2) \times V}{S} \quad (6)$$

where Z_1 and Z_2 are ozone concentrations at the inlet and outlet of the leaf chamber, V , gas flow rate, and S , leaf area. Eq-s (1 to 6) are given in their basic form. The correction terms were included in practical calculations to account for

the bulk flow of gas out of the leaf due to evaporation (Laisk, 1977; Parkinson and Penman, 1970).

Materials and Methods

Sunflower (*Helianthus annuus* L.) and *Perilla ocymoides* L. plants were grown in pots filled with soil on laboratory windows in summer. Upper full-grown leaves were used in experiments. The apparatus for measuring leaf CO_2 and water vapor exchange rates has been described by Oja (1983). For present experiments, a self-made corona-discharge ozone generator was added to the system. In principle, the apparatus contains two open systems for measuring leaf gas exchange (below referred to as channels) in which the gas composition can be adjusted independently by means of gas mixers MIX (Fig. 1). For adding CO_2 and O_3 , capillaries are used, and the rate of injection of these gases into the carrier gas stream is controlled by pressure differences on those capillaries. A sandwich type leaf chamber LC ($4.4 \times 4.4 \times 0.3 \text{ cm}$, flow rate $20 \text{ cm}^3/\text{s}$) can rapidly be switched into the chain of either the first or the second channel by the "channel exchange" valve. Infrared CO_2 analyzers "Infralyt IV" (GDR) are used for CO_2 , self-made

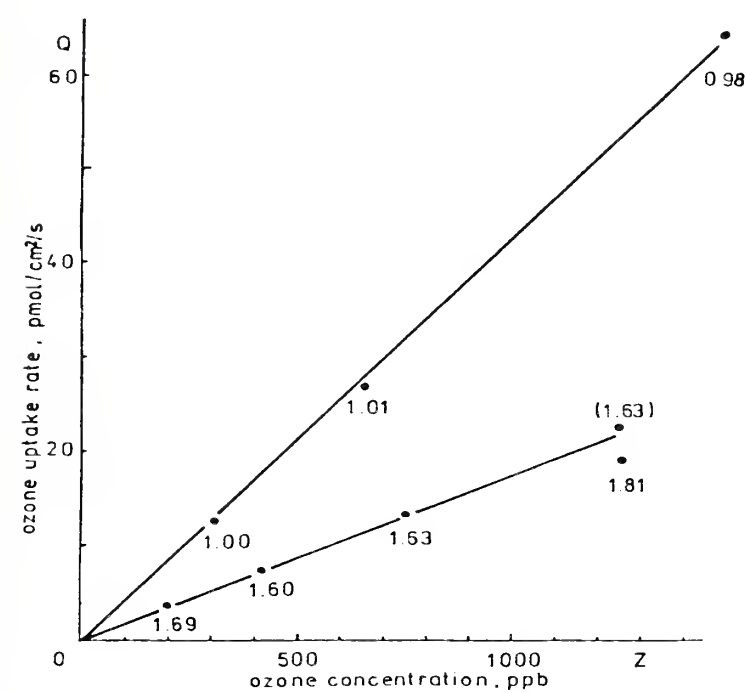


Figure 3. Dependences of ozone uptake rates *Q* on ozone concentration in two sunflower leaves

micropsychrometers for water vapor, and a Dasibi model 1003 AH analyzer for ozone. Volumes in the gas circuit are all reduced to the minimum. This guarantees a full-deflection response time of the system within 2.3 s (except for ozone).

Results

The measurement of the ozone uptake rate. A sunflower leaf was fitted into the leaf chamber,

and the chamber was connected to the channel containing no ozone; CO₂ concentration was 320 ul/l, irradiation density 30 mW/cm², leaf temperature 23°C. The chart recording of the psychrometer line reflected the time course of the stomatal opening, and the CO₂ uptake rate characterized photosynthesis (Fig. 2). At the same time, the ozone analyzer recorded the ozone concentration in the gas stream, as there was no leaf chamber in the circuit of that channel (a small drift was caused by the instabilities of the ozone generator). Periodically, the leaf chamber was “flopped over” to the channel with ozone (points denoted by A to H). Then the ozone concentration at the outlet of the leaf chamber rapidly declined showing its uptake by the leaf. There was a small uptake of ozone by chamber walls measured at A without a leaf.

The dependence of the ozone uptake rate on the ozone concentration was measured by changing the ozone concentration in the gas entering the leaf chamber (G, F, H. Fig. 2). The results are shown in Fig. 3, curve 1; another similar experiment is shown by curve 2. In the first experiment, the ozone uptake rate was exactly proportional to the ozone concentration. In curve 2, the point at the highest concentration declined from the proportionality, but the reason for this was an increase in the stomatal resistance (the values of the leaf gas phase

Table 1. Calculation of resistances and intercellular ozone concentrations for the experiment in Fig. 2.

Q is the ozone uptake rate; *r_{gw}*, leaf gas phase resistance for water vapor; *r_{gz}*, gas phase resistance for ozone calculated from *r_{gw}* (Eq. 4); *r_z*, resistance for ozone, calculated from the ozone uptake rate; *Z_i*, calculated ozone concentration in intercellulars.

Point	[O ₃] ppb	[O ₃] pmol/cm ³	<i>Q</i> pmol/cm ² /s	<i>r_{gw}</i> s/cm	<i>r_{gz}</i> s/cm	<i>r_z</i> s/cm	<i>Z_i</i> pmol/cm ³
A	723	29.0	1.058	-	-	27.5	-
B	733	29.42	6.13	4.15	6.93	4.83	- 4.59
C	691	27.77	12.36	1.55	2.59	2.28	- 1.32
D	665	26.32	14.81	1.22	2.04	1.85	- 1.66
E	675	27.12	16.51	1.07	1.78	1.69	- 0.35
F	660	26.52	16.51	1.01	1.69	1.66	0.43
G	306	12.30	7.96	1.00	1.67	1.59	- 0.16
H	1492	63.98	37.03	0.98	1.64	1.67	- 7.55

Table 2. The measurement of the intercellular ozone concentration in a sunflower leaf.

Ozone was supplied to the leaf from the lower side, and the evolution of ozone through the upper epidermis was measured. Denotations: r_{gw} , leaf gas phase resistance for water vapor; Q, ozone exchange rate.

Lower side of the leaf			Upper side of the leaf		
r_{gw} s/cm	$[O_3]$ ppb	Q pmol/cm ² /s	r_{gw} s/cm	$[O_3]$ ppb	Q pmol/cm ² /s
2.36	709	8.93	5.30	0	0
2.96	1790	17.96	4.17	0	0

resistance are shown at each point). After a correction for increased resistance, the point (in parentheses) fits well the proportionality. The proportionality between the ozone concentration and its absorption rate shows that the reaction of ozone degradation in leaf cells is a simple first-order reaction, and that it does not involve a saturating (enzymatic) process.

The dependence between conductances for ozone and water vapor. The first-order kinetics of ozone uptake justifies our application of the resistance/conductance approach and the calculation of total leaf conductances for ozone

$$g_z = \frac{Q}{Z_a} \tag{7}$$

where Z_a is the ambient ozone concentration, and Q is the uptake rate. In the linear-flow chamber, the ambient ozone concentration is

$$Z_a = \frac{Z_1 + Z_2}{2} \tag{8}$$

where Z_1 and Z_2 are concentrations at inlet and outlet ports. Combining Eq. (7) with Eqs. (6) and (8) we find

$$g_z = 2 \times \frac{Z_1 - Z_2}{Z_1 + Z_2} \times \frac{v}{S} \tag{9}$$

In our linear-flow chamber, $Z_2 = 0.5Z_1$ at the greatest stomatal openings, and the assumption that the ambient concentration is the arithmetic mean between the inlet and outlet is not absolutely correct, as the actual profile of concentration in the chamber is closer to exponential than to linear. Nevertheless, the error

caused by this assumption does not exceed 3% of g_z calculated from Eq. (9) (personal communication with V. Oja), and that correction term was also taken into account. The obtained values of r_z are given in Table 1.

From Fig. 2 one can see that the ozone uptake rate increases in parallel with the transpiration rate. The conductance for ozone $g_z = 1/r_z$ is plotted against the gas phase conductance $g_{gw} = 1/r_{gw}$ in Fig. 4. The relationship is fully linear up to the highest stomatal openings observed. The ozone conductance extrapolates to zero at a small value for ozone conductance. This residual conductance was mainly caused by the absorption of ozone by chamber walls and tubing (Fig. 2, A). After subtracting this conductivity (0.035 cm/s) from the total, the slope of the line does not change, but the interception point moves very close to the origin of

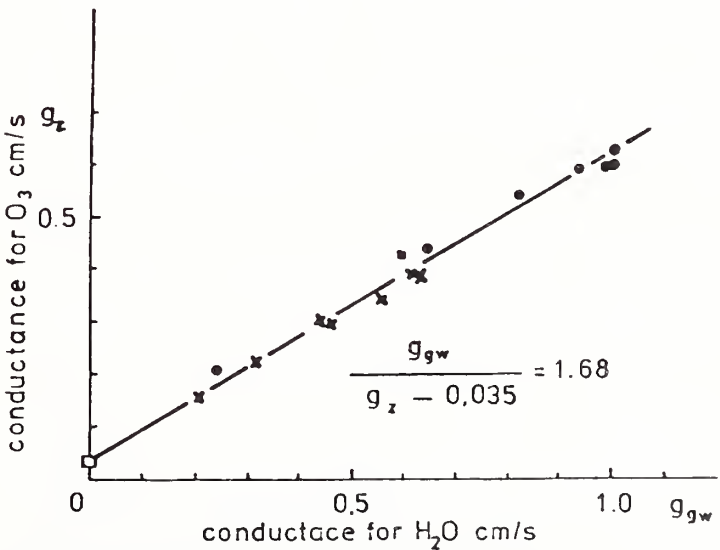


Figure 4. Relationship between the leaf gas phase conductance for water vapor g_{gw} and the conductance for ozone g_z in sunflower leaves

axes. Evidently, there was no, or there was very little, cuticular uptake of ozone observed in our experiments with sunflower leaves. The proportionality between the conductances for water vapor and ozone suggests that the diffusion paths for both gases fully coincide, and that there is no additional resistance for ozone in the liquid phase of cells. Evidently, ozone actively reacts with chemical substances in cell walls and plasmalemma, and it undergoes rapid degradation. This means that the ozone concentration in leaf intercellulars must be close to zero.

Ozone concentration in leaf intercellulars. Table 1 lists the values of the intercellular ozone concentration Z_i calculated from transpiration and ozone uptake rates and Eq. (5). Though there is some scattering of data, one can see that at different stomatal openings, Z_i stays quite close to zero independent of the ambient ozone concentration applied in the range up to 1.5 ppm.

Results given in Table 1 were obtained by using Eq. (4) and the calculated theoretical ratio of diffusion coefficients for water vapor and ozone. Actually, the diffusion rate will not depend only on the diffusion coefficient, but also on the dimensions of the diffusion pathway if the latter were getting close to the free path of molecules (so called Knudsen diffusion). The role of the Knudsen diffusion is quite difficult to estimate theoretically and, therefore, direct measurements of the ozone concentration in leaf intercellulars are welcome. The method applied below was first used by Oja (1972) for determining the CO_2 concentration in leaf intercellulars. If an amphistomatous leaf is exposed to ozone from one side, some of the ozone molecules should diffuse out from the leaf through the stomata of the other side if ozone concentration in intercellular spaces is different from zero. The measurements of the ozone evolution from that side provide information for calculating the real ozone concentration in intercellulars. To carry out this experiment, the

two-channel system (Fig. 1) was rearranged for using it together with a two-sided leaf chamber. One side of the chamber was connected into the circuit of one channel, and the other side into the other channel. Ozone was supplied into the gas stream at the physiologically lower side of the sunflower or perilla leaf while the ozone analyzer could be reswitched between the channels. Stomata on both sides of the leaf were open enough to allow a sufficient ozone exchange. There occurred a significant ozone uptake from the lower leaf side, but no ozone evolution through the upper epidermis was detected in a sunflower (Table 2) as well as in a Perilla leaf (data not shown). This shows that the ozone concentration is really negligibly low in intercellular air spaces at the substomatal cavities of the upper side of the leaf in case ozone is supplied from the lower side.

Discussion

From these results, we can conclude that ozone enters the leaf through stomata by diffusion; it confirms a more indirect evidence (Guderian *et al.*, 1987; Skarby *et al.*, 1987), and is in accordance with conclusions drawn by Heath (1980) in his review. The ozone concentration in intercellular spaces is extremely low irrespective of the ambient concentration of ozone applied (up to 1.5 ppm). This means that ozone is absorbed and rapidly decomposed in cell walls or plasmalemma region, and it does not penetrate into the deeper layers of cells. The ozone uptake rate Q can be calculated from the conductance for water vapor and the ratio of the measured diffusion rates for water vapor and ozone as

$$Q = Z_a \times g_{gw} / 1.68 \quad (10)$$

where Z_a is the ambient ozone concentration, and g_{gw} , the gas phase conductance for water vapor. Moldau and Sober (personal communication) found a significant component of transpiration in bean leaves that was not accompanied by the proportional ozone uptake, and they

identified it as the cuticular transpiration. In our experiments with short-time exposures to ozone, the cuticular transpiration of sunflower leaves was either very small, or it was accompanied by cuticular ozone uptake. Probably long exposures under high ozone concentrations damage cuticula causing increased cuticular transpiration.

There occurred no detectable ozone flux through the leaf which may mean that ozone is rapidly decomposed already in stomatal pores or substomatal cavities. The rapid decomposition of ozone must cause oxidation processes which damage cell walls and plasmalemma. The reflection coefficients of plastid membranes were reduced in the presence of ozone, the introduction of ozone into a culture of *Chorella* cells caused a 15- to 20-fold increase in the efflux of potassium (review in Heath, 1980). Sober (in press) has shown that the properties of the cell walls and/or plasmalemma of bean leaves changes after rather short exposures to ozone. The elasticity modulus of the walls increased, the stretchability of cells decreased.

The tolerance of plants to ozone has two different mechanisms. One is based on the stomatal closure in response to higher ozone concentrations and operates on the basis of suppressing the ozone flux into the leaf. This brings along a considerable reduction in the CO_2 uptake rate and a decrease in the growth rate and plant yield. The other way to withstand higher ozone concentrations is to develop a mechanism for the neutralization of the damage caused by ozone for living cells. Evidently, this mechanism involves the resynthesis of damaged enzyme molecules or membrane fractions, and it causes increased maintenance/reparation energy costs accompanied by higher respiration rates (Skarby *et al.*, 1987; Heath, 1980). In future perspectives, the studies of the effect of ozone on plants should lead to the establishment of a reparation cost of one ozone molecule in a number of respired CO_2 molecules.

Acknowledgements

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Literature Cited

- Chen, N.H., and D.F. Othmer. 1962. *J. Chem. Eng. Data* Vol. 7, 1: p. 37.
- Guderian, R. *et al.* 1987. Effects of photochemical oxidants on plants. *Ecol. Studies* 52.
- Heath, R.L. 1980. Initial events in injury to plants by air pollutants. *Ann. Rev. Plant Physiol.* 31:395-431.
- Hodgman, C.D., R.C. Weast, and S.M. Selby. 1955-1956. *Handbook of Chemistry and Physics*. Ed. 37. Chemical Rubber Pub. Co., Cleveland, Ohio, p. 2121.
- Kress, L.V., and J.M. Skelly. 1982. Response of several eastern forest tree species to chronic doses of ozone and nitrogen dioxide. *Plant Dis.* 12:1149-1152.
- Laisk, A. 1977. *Kinetics of photosynthesis and photorespiration in C_3 plants*. Publ. House Nauka, Moscow (in Russian).
- Lehnherr, B., A. Grandjean, F. Machler, and J. Fuhrer. 1987. The effect of ozone in ambient air on ribulosebiphosphate carboxylase/oxygenase activity decreases photosynthesis and grain yield in wheat. *J. Plant Physiol.* 130:189-200.
- Miller, P.R., O.C. Taylor, and R.G. Wilhour. 1982. Oxidant air pollution in the central valley, Sierra Nevada foothills and Mineral King valley of California. *Atmos. Environ.* 6:623-633.

- Oja, V. 1972. *Experimental studies of the CO₂ gas exchange in plant leaves*. Cand. thesis. Institute of Astrophysics and Atmospheric Physics, Estonian Acad. Sci. Tartu (in Russian).
- Oja, V. 1983. A quick-operating gas measuring device for studying the kinetics of leaf photosynthesis. *Fiziologia Rastenii* (Soviet Plant Physiol) 30:1045-1052 (in Russian).
- Parkinson, K.J., and H.L. Penman. 1970. A possible source of error in the estimation of stomatal resistance. *J. Exptl. Bot.* 21:405-409.
- Skarby, L., E. Troeng, and C-A Bostrom. 1987. Ozone uptake and effects on transpiration, net photosynthesis, and dark respiration in Scotch pine. *Forest Sci.* 33:801-808.
- Sober, A. Effects of ozone on water relations in bean leaves. *Plant Physiol.* (in press).
- Weast, R.C., ed. 1982-1983. *Handbook of Chemistry and Physics*. Ed. 63 CRC Press, Boca Raton, Florida.

Legends to Figures

Fig. 1. Basic circuit of the two-channel leaf gas exchange measurement system. LC, leaf chamber; MIX1 and MIX2, gas mixers; C₁ and C₂, different CO₂, O₂, O₃ and water vapor concentrations in the gas mixtures; CH EXCH, channel exchange valve for connecting the leaf chamber into the circuit of either channel 1 or channel 2; EQ, an equivalent resistance to the leaf chamber; EX, exit valves for flushing the leaf chamber after channel exchanges; GA, infrared gas analyzers; PS, psychrometers; OA, ozone analyzer.

Fig. 2. Parallel measurement of photosynthesis, transpiration and ozone uptake in a sunflower leaf. E, transpiration rate, nmol/cm²/s; P, CO₂ uptake rate, nmol/cm²/s; Z, ozone concentration, ppb, recorded by the ozone analyzer. In A to H, the leaf chamber was connected into the gas stream of the channel containing ozone for about 3 min. In A, the chamber was empty, before G the background ozone concentration was decreased to 400 ppb, before H increased to 1930 ppb (note that at H the range of the analyzer extends from 1000 to 2000 ppb). Leaf temperature 23.1°C, PhAR density 30 mW/cm².

Fig. 3. Dependences of ozone uptake rates Q on ozone concentration in two sunflower leaves. Leaf gas phase resistance, s/cm shown at each point.

Fig. 4. Relationship between the leaf gas phase conductance for water-vapor g_{gw} and the conductance for ozone g_z in sunflower leaves. Circles are from the experiment in Fig. 2, crosses are from other experiments; square denotes ozone absorption by chamber walls.

Ozone and the Winter Injury Hypothesis in Forest Decline

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It has been proposed that forest declines in both Western Europe and North America are caused by the interaction of multiple stresses. One expression of this phenomenon appears to be an alteration in foliar resistance to frost damage or winter desiccation (Johnson and Siccama, 1983, 1984; Friedland *et al.*, 1984; Blank, 1985; Rehfuss, 1987; Johnson *et al.*, 1988). In Germany, it has been suggested that ozone plays a central role in the decline phenomenon (Rehfuss, 1987) and accumulating experimental evidence suggests that this may be true. Brown *et al.* (1987) found that exposure of Norway spruce seedlings to ozone levels, which produced no visible symptoms during the growing season, reduced the subsequent frost resistance of certain clones during the following autumn. Air pollutants, then, may act to impair the physiological activities which underlie seasonal rhythms of active growth, dormancy and hardening (Davison and Barnes, 1987). However, to date little has been established concerning effects of ozone on specific physiologi-

cal changes associated with the onset of dormancy and cold tolerance.

Aronsson *et al.* (1976) demonstrated a strong correlation of frost hardiness with changes in the foliar carbohydrate content of both pine and spruce (see also Parker, 1959). Growth reductions in declining stands of Norway spruce have been attributed to changes in carbohydrate source-sink relations (Oren *et al.*, 1988) and Bosch *et al.* (1983) showed that needles harvested in November from declining trees had relatively higher starch and lower raffinose levels than did comparable needles from healthy trees. Because raffinose and other soluble sugars are believed to act as foliar cryoprotectants, an alteration in the amount or rate of production of these compounds may lead to increased sensitivity to subfreezing temperatures.

We are accumulating evidence that supports the role of ozone exposure in altering winter hardening processes in red spruce seed-

lings. Seedlings exposed to levels of ozone ranging from 0.4 to 3.0 times ambient ozone levels in Ithaca, New York, USA, exhibited no detectable changes in physiology during the season of active growth. However, in December, significant anatomical alterations were found in spite of the fact that no classic visible symptoms appeared on the current year foliage. A cross-section from a needle of a seedling grown in charcoal-filtered air taken in December showed that many of the vacuoles were filled with tannins and multiple layers of chloroplasts were present (Plate 1). In contrast, histological examination of needles taken from the 3 times ambient treatment indicated extensive damage had occurred to mesophyll cells (Plate 2). This damage included vesiculation and, at its most extreme, total disruption of cells with breakage of cell walls and leakage of contents into inter-cellular spaces. A damage index based on the proportion of cells injured in cross-sections of these needles indicated that the proportion of cells disrupted increased with increasing ozone dose ($P = 0.0175$). Disruption of this nature was not seen earlier in the season prior to freezing temperatures, and is hence considered to be frost damage.

In contrast to the histological evidence, analysis of foliar pigments in December did not exhibit any pattern suggestive of an ozone-

freezing temperature interaction (Figures 1-3). Following one winter in the field, however, chlorophylls a and b and carotenoids exhibited trends which suggest that ozone exposure prior to overwintering exacerbates the normal loss of pigments which occur during exposure to freezing temperatures (Figures 1-3).

Polynomial regression analysis of the starch and soluble sugar content of foliage over the seven-month exposure period indicated that there was a trend that was not statistically significant for decreased rate of change in the total soluble carbohydrate pool in current year needles (Table 1). In support of this finding, the linear rate of accumulation of the sugar raffinose during the fall was found to be significantly reduced in trees exposed to ozone ($P = 0.046$; Table 1). As such, it appears that ozone exposure may impair normal carbohydrate metabolism in foliage of red spruce seedlings, which may contribute to their increased susceptibility to frost damage. It should be noted that, for the entire population of seedlings, severe winter injury symptoms, loss of foliage or necrosis of the current year's foliage, did not develop in any pattern suggesting an ozone-mediated response. However, of those plants that were damaged, there was a significant quadratic relationship between the natural logarithm of the number of flushes with necrotic needles and

Table 1. Parameter estimates for needle soluble sugar cycling during seven months exposure to ozone.¹

ozone treatment	total soluble sugars		raffinose	
	linear	quadratic	linear	quadratic
cf	8.08	0.744	0.568	0.154
1x	7.59	0.558	0.323	0.444
2x	7.31	0.448	0.449	0.872
3x	7.49	0.461	0.028	0.561
LSE ²	0.44	0.094	0.136	0.275
Probability ³	0.343	0.058	0.046	0.163

1 Parameter estimates for total soluble sugars determined from cubic polynomial regression over time; estimate for raffinose determined from quadratic polynomial regression over time.

2 LSE = standard error of least square mean estimates.

3 Probability of parameter estimates following linear dose-response to increasing ozone.

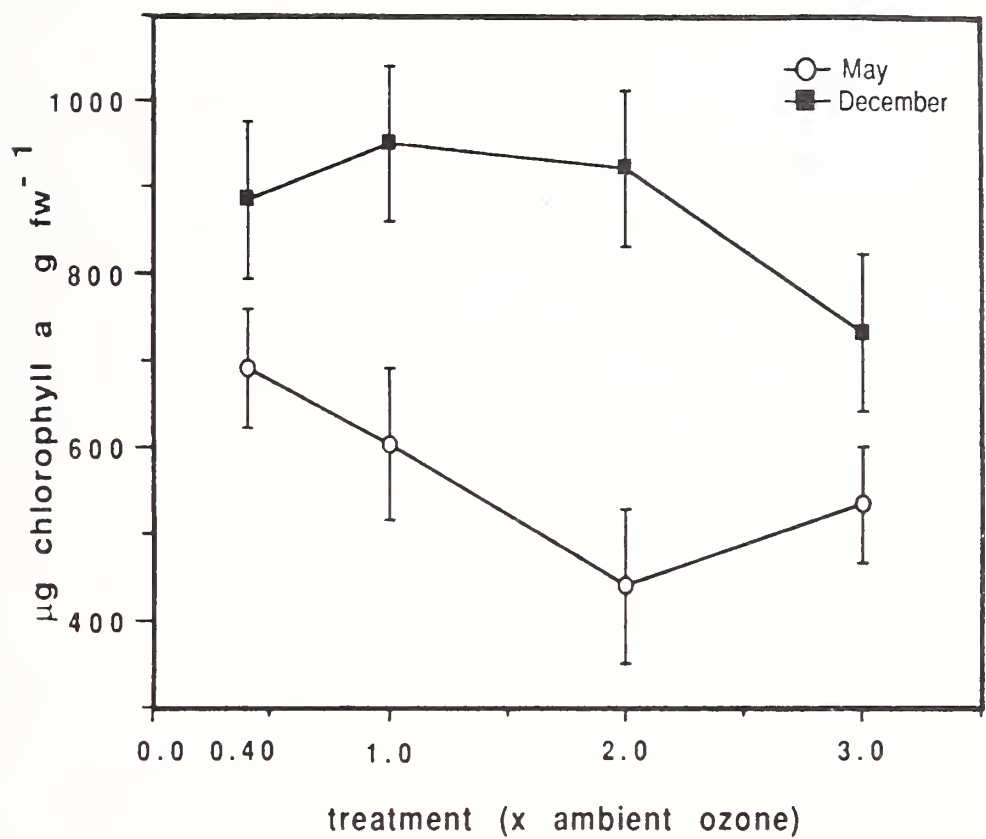


Figure 1. Effect of ozone exposure on chlorophyll a content of red spruce seedling foliage in December following fumigation and in May after overwintering following exposure.

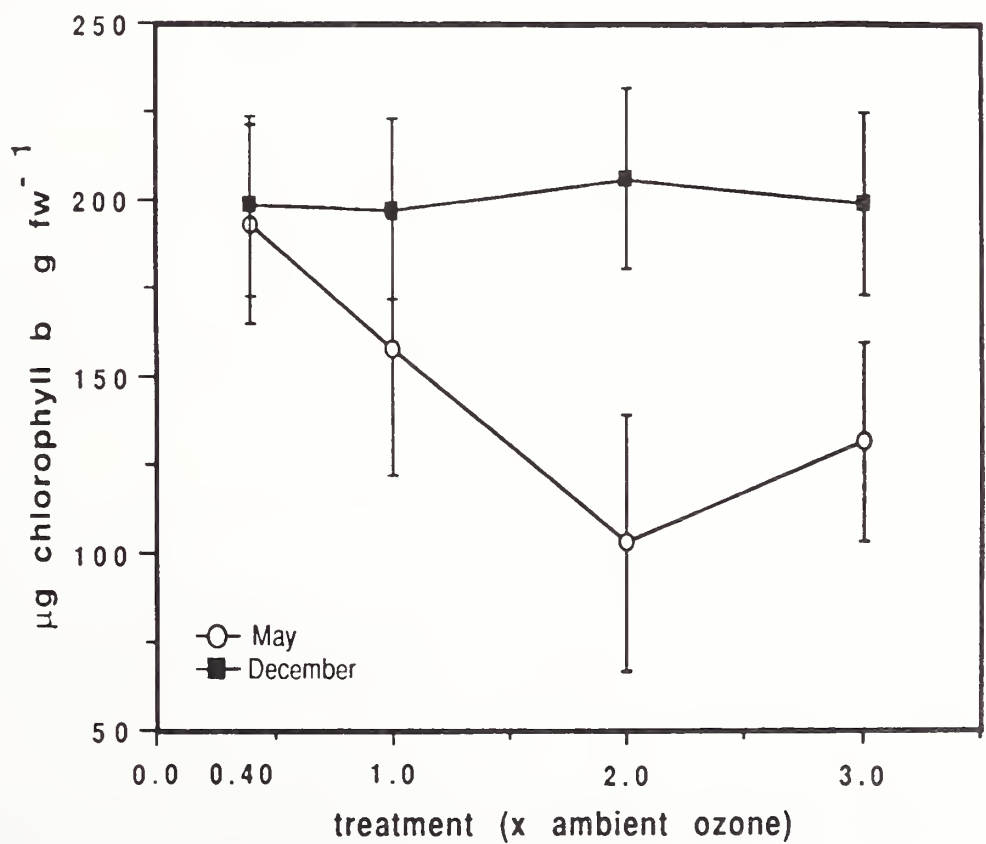


Figure 2. Effect of ozone exposure on chlorophyll b content of red spruce seedling foliage in December following fumigation and in May after overwintering following exposure.

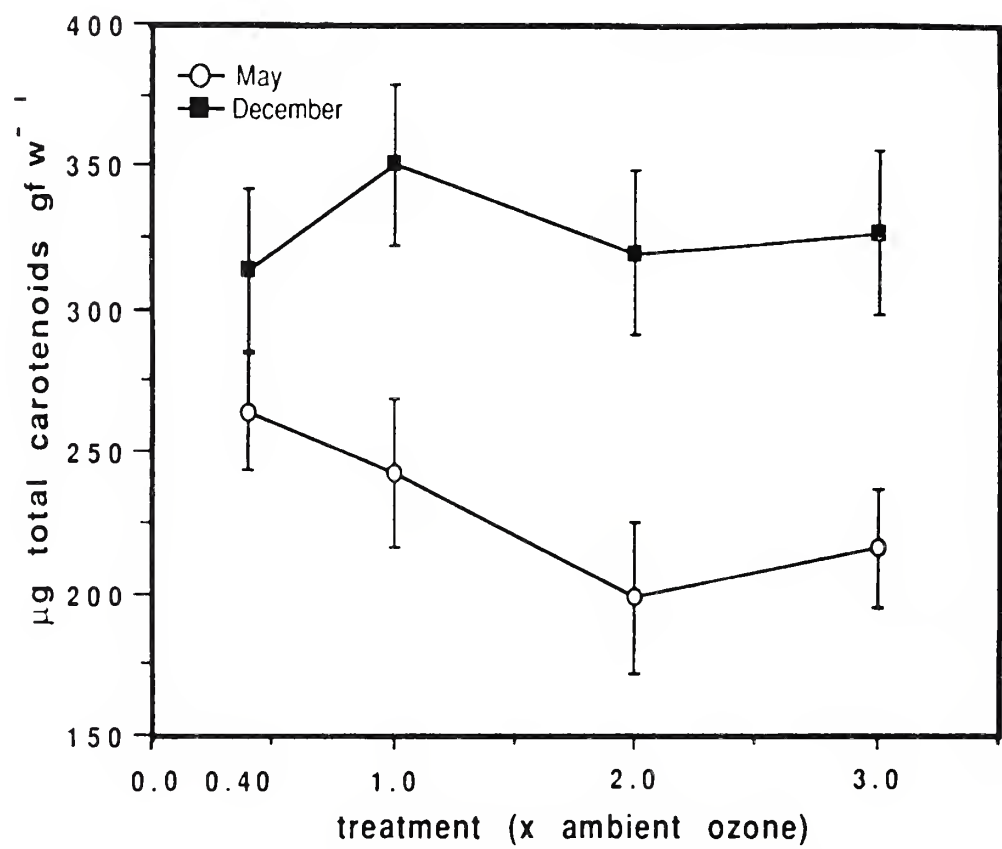


Figure 3. Effect of ozone exposure on total carotenoid content of red spruce seedling foliage in December following fumigation and in May after overwintering following exposure.

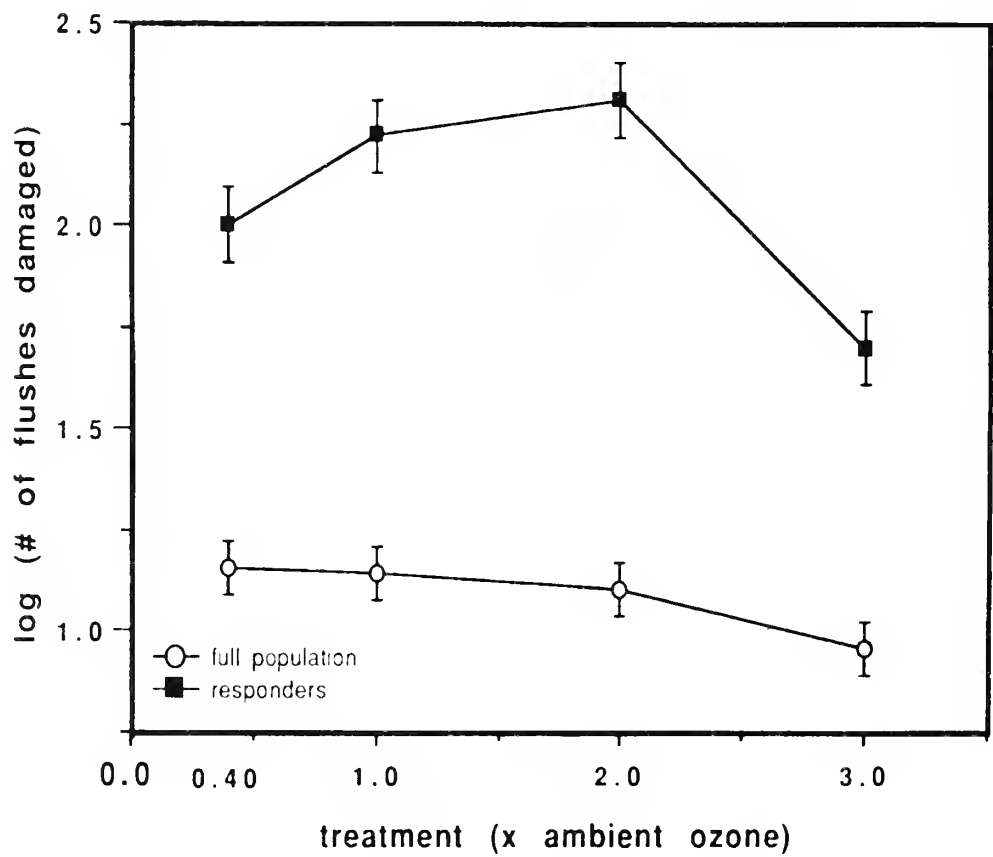


Figure 4. Effect of ozone exposure on number of flushes in red spruce seedlings with necrotic needles in early spring. The assessment was made prior to bud break on flushes that developed during ozone exposure in the previous season. A flush was considered necrotic if any of the needles exhibited browning.

ozone level (Figure 4).

The winter hardening process includes the breakdown of accumulated starch to form raffinose and other soluble sugars which act as cryoprotectants (Little, 1970; Senser *et al.*, 1971, 1975; Soikkeli, 1978). Bosch *et al.* (1983) found higher levels of starch in the needles of declining trees in the autumn, suggesting that the transition from the frost-sensitive to frost-tolerant state is impaired in declining trees. Whether this is the result of exposure to airborne pollutants leading to increased frost damage and decline, or simply a secondary symptom of declining trees is yet to be elucidated. The ultrastructural evidence suggests that ozone-exposed needle cells were more susceptible to winter injury than were cells from needles in the charcoal-filtered environment. It is hypothesized that ozone alters carbohydrate metabolism during the early phase of winter hardening and results in a delay in the increase in cryoprotectants. Cells, which were unprepared for the subfreezing temperatures of late October and November, would be more susceptible to frost injury. Although the root cause of this effect of ozone is not yet apparent, some direct effect on the initiation of hardening is possible.

Literature Cited

- Aronson, A., T. Ingestad, and L. Lars-Gorau. 1976. Carbohydrate metabolism and frost hardiness in pine and spruce seedlings at different photoperiods and thermoperiods. *Physiologia Plantarum* 36:127-132.
- Blank, L.W. 1985. A new type of forest decline in Germany. *Nature* 314:311-314.
- Bosch, C., E. Pfannkuch, U. Baum, and K.E. Rehfuss. 1983. Über die Erkrankung der Fichte (*Picea abies* Karst) in den Hochlagen des Bayerischen Walden. *Forstw. Clb.* 102:167-181.
- Brown, K.A., T.M. Roberts, and L.W. Blank. 1987. Interaction between ozone and cold sensitivity in Norway spruce: a factor contributing to the forest decline in Central Europe? *New Phytologist* 105:149-155.
- Davison, A.W., and J.D. Barnes. 1988. How are the effects of air pollutants on agricultural crops influenced by the interaction with other limiting factors? Effects of winter stress on pollutant responses. In *Proceedings, 1986 Commission of the European Communities and the National Agency of Environmental Protection; 1986 March 23-25; England*, in press.
- Friedland et al. 1984. Winter damage to foliage as a factor in red spruce decline. *Canadian Journal of Forest Research* 14:963-965.
- Johnson, A.H., E.R. Cook, and T.G. Siccama. 1988. Relationships between climate and red spruce growth and decline. *Proc. Nat. Academy Sci.*, in press.
- Johnson, A.H., and T.G. Siccama. 1983. Acid deposition and forest decline. *Environmental Science and Technology* 17:A294-A305.
- Johnson, A.H., and T.G. Siccama. 1984. Decline of red spruce in the northern Appalachians: assessing the possible role of acid deposition. *Tappi Journal* 67:68-72.
- Little, C.H.A. 1970. Seasonal changes in carbohydrate and moisture content in needles of balsam fir (*Abies balsamea*). *Canadian Journal of Botany* 48:2021-2028.
- Oren, R., E.-D. Schutze, K.S. Werk, J. Meyer, B.U. Schneider, and H. Heilmeyer. 1988. Performance of two *Picea abies* (L.) Karst stands at different stages of decline. *Oecologia* 75:25-37.
- Parker, J. 1959. Seasonal variation in sugars of conifers with some observations on cold resistance. *Forest Science* 5:56-63.
- Rehfuess, K.E. 1987. Perceptions on forest diseases in Central Europe. *Forestry* 60(1):1-11.
- Senser, M., and E. Beck. 1984. Correlation of chloroplast ultrastructure and membrane lipid composition to the different degrees of frost resistance achieved in leaves of spinach, ivy, and spruce. *J. Plant Physiol.* 117:41-55.
- Senser, M., F. Schotz, and E. Beck. 1975. Seasonal changes in structure and function of spruce chloroplasts. *Planta (Berlin)* 126:1-10.
- Senser, M., P. Dittrich, O. Kandler, A. Thanbichler, and B. Kuhn. 1971. Isotopenstudien über den Einfluss der Jahreszeit auf den Oligosaccharidumsatz bei Coniferen. *Ber. Dtsch. Bot. Ges. Band* 84:445-455.

Soikkeli, S. 1978. Seasonal changes in mesophyll ultrastructure of needles of Norway spruce (*Picea abies*). *Canadian Journal of Botany* 56:1932-1940.

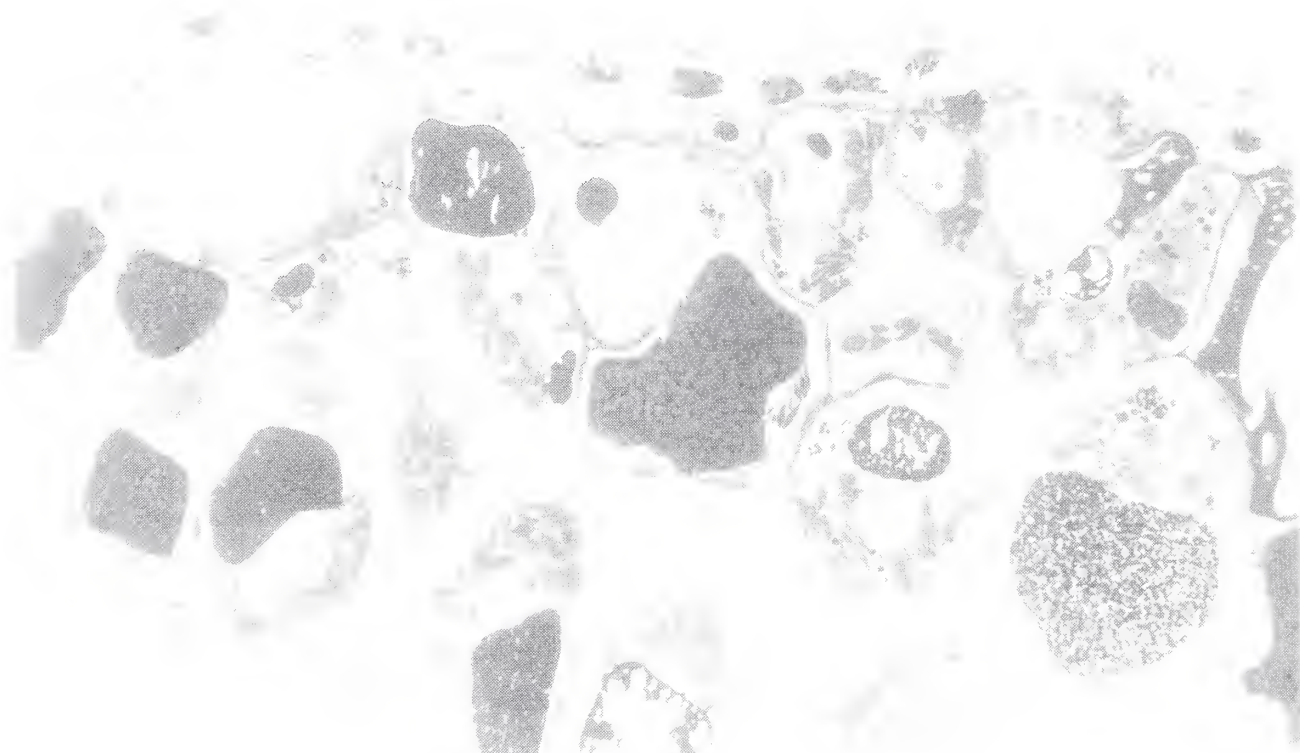


Plate 1. A cross-section from a needle of a seedling grown in charcoal-filtered air taken in December.

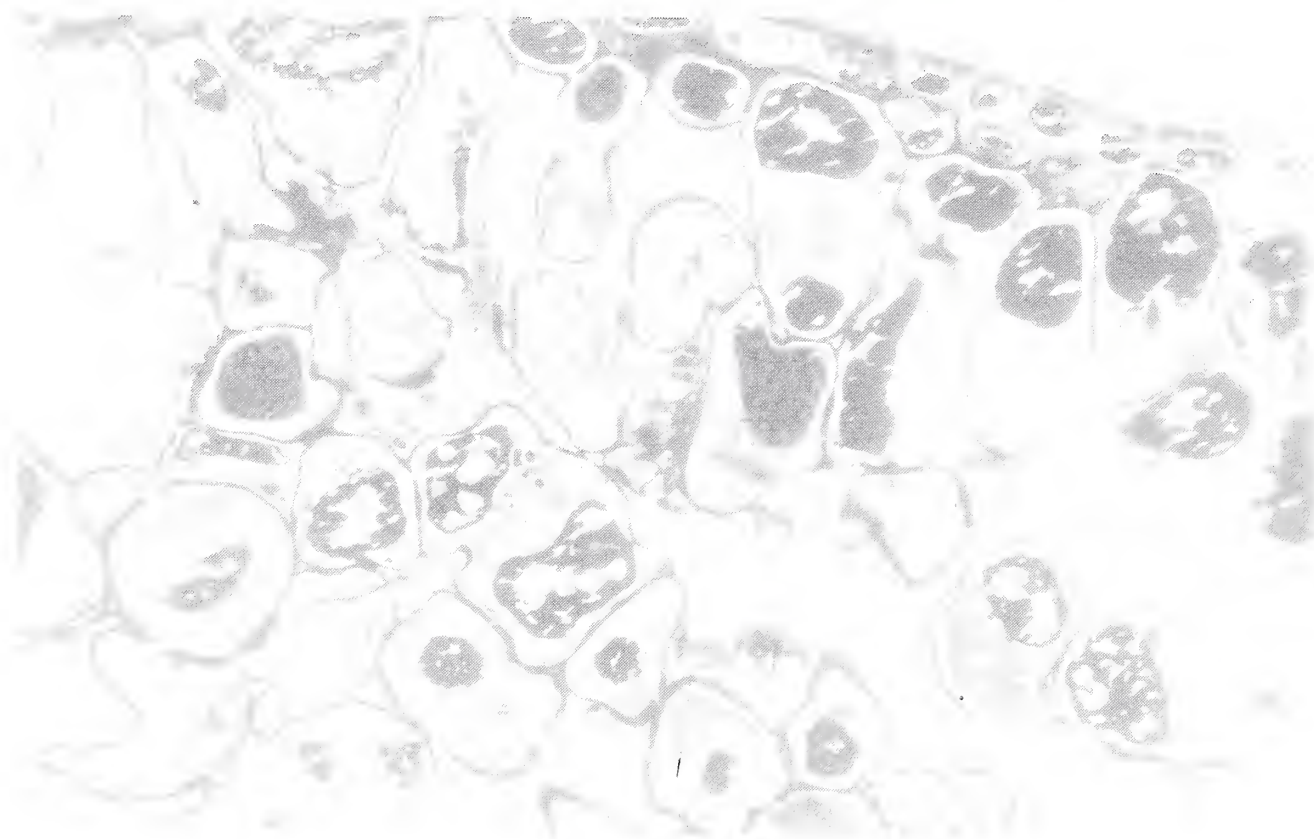


Plate 2. Needles taken from the 3 times ambient treatment indicated extensive damage had occurred to mesophyll cells .

Comparative Physiology and Morphology of Seedling and Mature Forest Trees

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Introduction

Much of the knowledge which has been gained in the past decades concerning physiological responses of forest tree species to their environment has come from studies of tree seedlings. This is particularly true in the study of atmospheric pollutants since controlled exposure of large, mature trees poses many logistical problems. Although most of the experimentation in environmental physiology has been conducted on seedlings, there is concern whether the information can be used to make interpretations for trees in other stages of development. Thus, one of the important problems facing researchers is determining in what respects seedlings and mature trees are similar in their responses to the environment.

The objective of this paper is to highlight differences in the ecophysiology of seedlings and trees which must be considered when comparing their physiological or morphological responses of seedlings and mature trees to environmental stimuli. This discussion is not intended to be an exhaustive literature review of seedling and mature tree physiology, but rather, to point out how tree aging and development might impact the extrapolation of data gathered using seedlings.

Definitions

According to Harlow and Harrar (1979) a tree is defined as "... a woody plant which at maturity is 20 feet (6.1 m) or more in height with a single trunk, unbranched for at least several feet above the ground, and having a more or less definite crown." While most foresters and plant scientists have a good notion of whether to call a plant a seedling or a mature tree, there are few formal definitions in the literature. For the purposes of the present discussion, we shall consider a seedling to be a tree which has germinated from a seed (i.e. not a root sprout or cutting), and is less than three years old. A mature tree is defined here as a tree which possesses one or more of the mature traits of that species, such as cone or flower production, natural pruning of lower branches, or the production of mature wood. Trees which do not fit into the either category are defined as saplings and will not be considered in this article.

Morphological Considerations

The most obvious differences between seedlings and trees are those dealing with scale. Seedlings, as we are considering them here, are typically less than one meter tall and

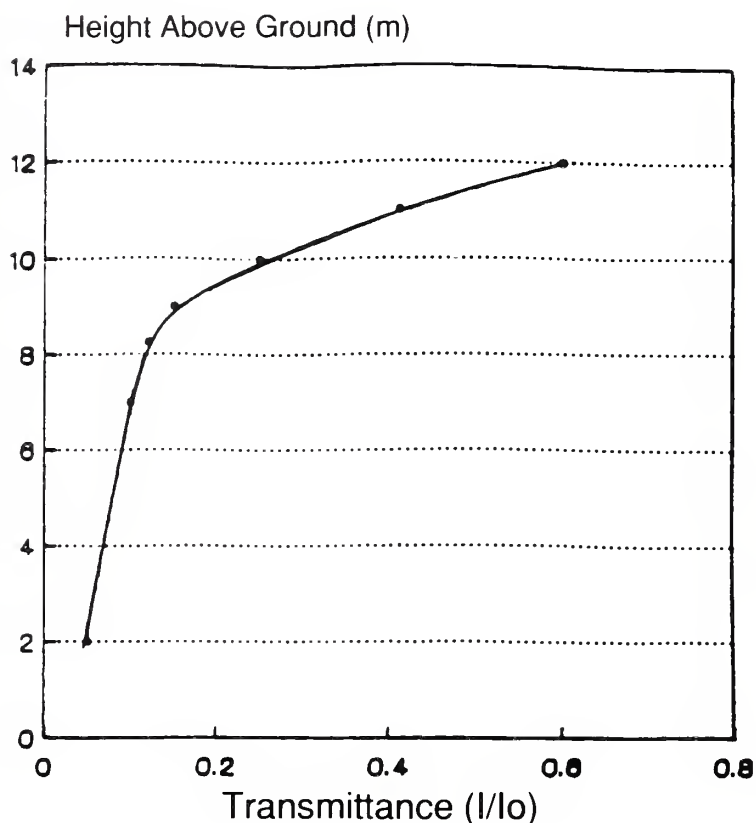


Figure 1. Patterns of photosynthetically active radiation (PAR) through a *Pinus taeda* canopy. Adapted from Sinclair and Knoerr, 1982.

have had distinct branch morphology for one or two years. Mature trees, in contrast, may range from 6 meters to over 100 meters for coast redwood (*Sequoia sempervirens* (D. Don) Endl.), and typically have a well defined branch architecture. Light patterns through a tree canopy within the forest usually follow a defined pattern depending on the architecture of the species. Sinclair and Knoerr (1982) examined the patterns of photosynthetically active radiation (PAR) in the canopy of a fifteen-year-old plantation of loblolly pine (*Pinus taeda* L.). As shown in Figure 1, the proportion of incident radiation observed at a given level relative to the PAR at the top of the canopy (I/I_o) decreased in a curvilinear pattern down through the canopy.

Distinct differences in the morphological and physiological characteristics of tree foliage which may impact gas exchange and the uptake of gaseous pollutants are associated with canopy position (Kramer and Kozlowski, 1979). For example, Wong and Dunin (1987) found that the maximum rate of photosynthesis of

mature sun leaves (upper canopy) of *Eucalyptus maculata* Hook. was more than two times that of shade leaves (lower canopy). Boardman (1977) has reported that chlorophyll content and chloroplast structures differ in shade leaves as compared to sun leaves. Other differences include changes in specific leaf weight, stomatal density, RUBP concentration, number of palisade layers, cuticle thickness and rates of respiration.

Sun and shade leaf variation in seedlings is small due to lack of mutual shading. However, pronounced differences exist in the morphology and physiology of primary and secondary foliage of certain conifers. Loblolly pine seedlings, for example, have two distinct phases of growth. Prior to the formation of the first terminal bud, a loblolly pine seedling undergoes a free growth phase. Subsequent to the formation of the first terminal bud, the seedling enters the cyclic growth phase (Williams, 1987). Shoot ontogeny of first year growth includes seed germination, cotyledon emergence, primary needle formation, and subsequently, secondary needle formation. The primary needles are singular while the secondary needles are arranged in fascicles of three. For most species, it is common for seedlings to have multiple periods of foliage expansion within a single year, while in trees, the number of these periods is greatly reduced. During the growth of foliage, the development of the cuticle and changes in stomatal activity occur. These ontogenic changes are important to consider when studying the responses of seedlings and trees to airborne pollutants since the responses will affect the amount absorbed by the foliage.

The rate of primary needle expansion in red pine (*P. resinosa* Ait.) is dependent on the photosynthetically active tissues of the cotyledons (Sasaki and Kozlowski, 1970). Bormann (1956) showed that young pine seedlings with both primary and secondary needles reached maximum rates of photosynthesis at lower light intensity than those with predominantly second-

dary needles. In trees, maximum rates of photosynthesis are obtained in current year foliage that has fully expanded (Brix, 1971; Rook and Carson, 1978).

Estimates of the number of stomata per leaf indicate large variations in the number of stomata per leaf of seedlings and trees due to both genetic and environmental influences. A study by Knauf and Bilan (1974) directly compared the number of stomata between two-year-old seedlings and sixteen-year-old loblolly pine trees. The mature trees had approximately twice the stomata per leaf than the seedlings due to an increased number of stomata per square millimeter and an increase in the total surface area of the leaves. Other studies have reported densities between 141-161 stomata mm^{-2} surface area for trees and 138-180 stomata mm^{-2} surface area for seedlings (Higginbotham, 1974; Thames, 1963). However, it should be pointed out that even though the stomatal density may not differ between the seedlings and the trees, the overall number of stomata will increase with maturity due to an increase in leaf area. These differences could potentially impact the uptake of an air pollutant because the stomates represent the point of entry of gases into the plant. Positive correlations have been demonstrated between ozone sensitivity and stomatal conductances in a number of tree species (Reich and Amundson, 1985).

In addition to differences in foliage, seedlings and mature trees have roots with different abilities to exploit below ground resources. The water relations of seedlings are often tightly coupled to the amount of available moisture in the uppermost layers of soil. This coupling tends to decrease as seedlings age. Sands and Nambiar (1984) examined the water relations of *Pinus radiata* D. Don seedlings planted in three consecutive years, with and without weed control. No differences were found in the diurnal patterns of xylem pressure potential (XPP) between the seedlings that had been planted in

three years on the weed-controlled and non-controlled plots. However, seedlings that had been in the field for only one or two years had consistently more negative XPP when grown in competition with weeds. This indicates that the younger seedlings were unable to utilize water sources which were available to the three-year-old plants.

The differences in seedling and mature tree rooting intensity and rooting volume will also result in differences in their capacity to extract nutrients from the below ground environments. In addition, the supply and demand for nutrients vary with stand development. Allen *et al.* (1988) presented a conceptual analysis of nitrogen supply and demand over the course of a typical rotation for *P. taeda* (Fig. 2). Several key points emerge from this diagram. Initially, the nitrogen supply of the site exceeds the requirements of seedlings for nitrogen. However, as the stand ages, the demand for nitrogen increases while the ability of the site to supply nitrogen decreases. This results in a deficit of available nitrogen to meet the demands of tree growth. Figure 2 also indicates that as the stand ages, internal remobilization of nitrogen becomes increasingly important. This represents a key difference in the response of seedlings and trees because stresses such as drought or air pollution often cause an increase in the rate of leaf senescence. If early senescence alters the amount of nitrogen which is remobilized, it will significantly reduce the nutrient supply for subsequent growth.

Another important morphological difference between seedlings and trees, particularly in conifers, is the change which occurs in conducting elements as a tree matures. Figure 3 shows the relationship of earlywood to latewood production with age for *P. echinata* Mill. Earlywood cells are thin-walled and have large diameters and, therefore, have a greater capacity for conducting water than thicker-walled latewood cells. For seedlings of *P. echinata*, the percent of latewood in the annual ring may be as

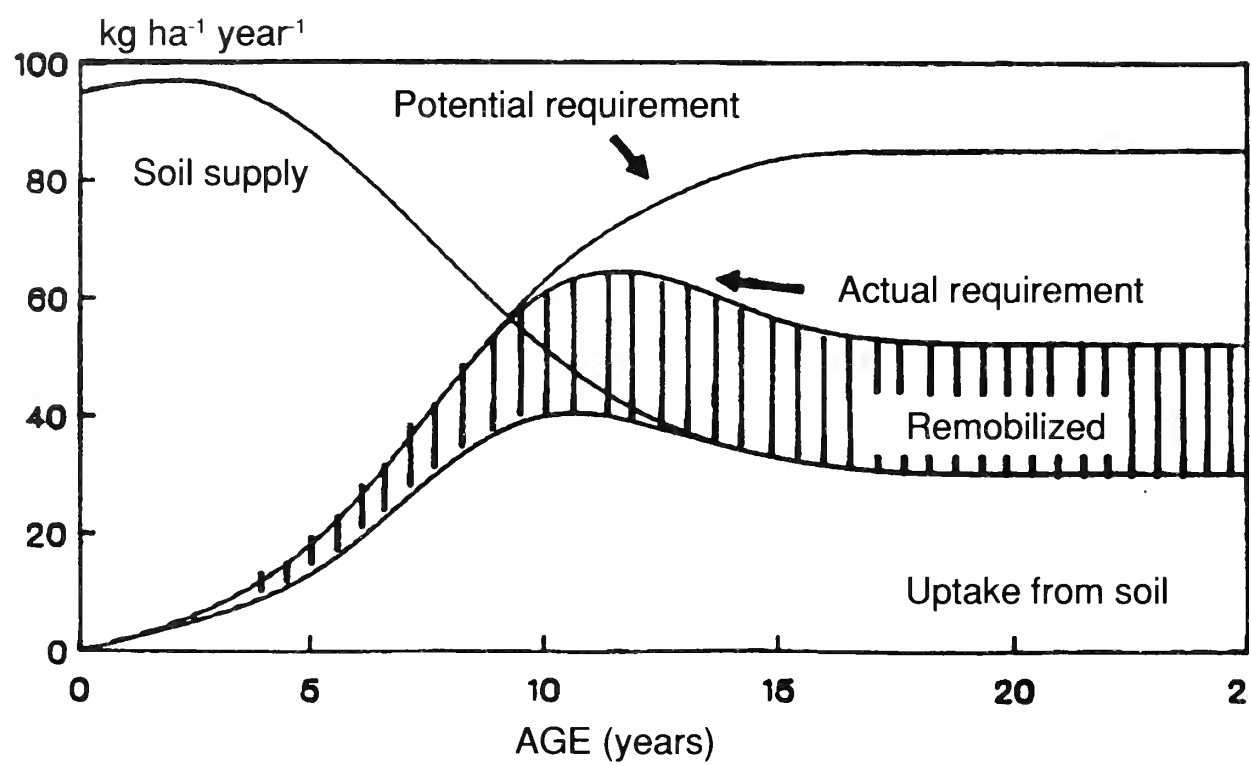


Figure 2. Conceptual relationship of soil nitrogen supply, remobilization and demand. Adapted from Allen *et al.*, 1988.

low as 15 percent, while the latewood ratio may be over 60 percent for trees older than 25 years. Such large differences in the mature conducting elements can be expected to exert a profound influence on resistance to flow and the patterns of water movement of the plants. Since specific

gravity is linearly related to the percent latewood in most species, changes in specific gravity may be inversely related to changes in conductivity of xylem elements. Panshin and de Zeeuw (1980) reported that in most tree species, the mature and juvenile xylem differ in

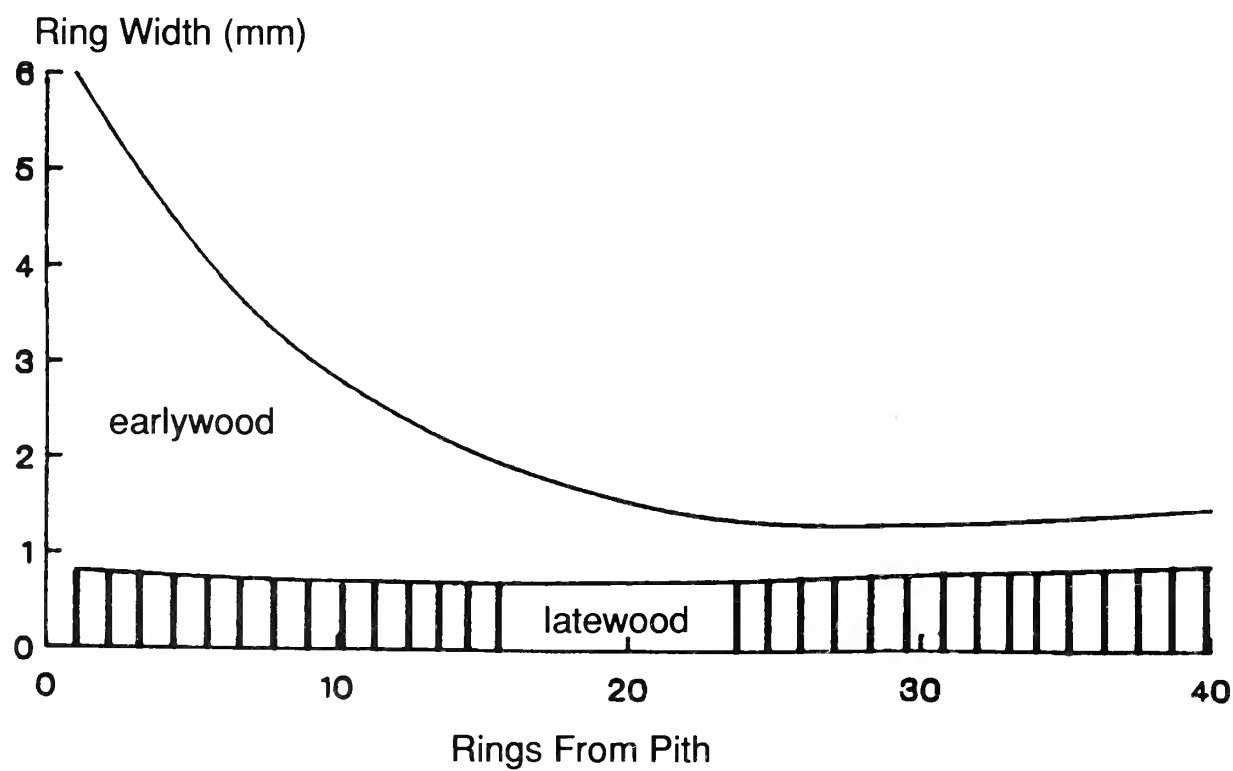


Figure 3. Relationship of earlywood and latewood with age for *Pinus echinata*. Adapted from McGinnes, 1963.

specific gravity.

Physiological Considerations

Many of the differences in seedling and mature tree morphology greatly impact physiological processes. Some of the processes in which seedlings and trees may differ include photosynthesis, water relations, and translocation.

Photosynthesis

As discussed earlier, one of the primary differences between seedlings and trees with regard to photosynthesis is the variation between sun and shade foliage. In seedlings, relatively little mutual shading occurs, resulting in primarily sun foliage, while in trees, a mosaic of foliage types occurs. Given that shade foliage has a lower photosynthetic capacity than sun foliage, it may be expected that in seedlings, the rate of photosynthesis per unit leaf area will tend to be greater than that for mature trees. Halpin (unpublished data) measured rates of net C°2 exchange of seedlings and twelve year-old trees of *P. taeda* on the University of Georgia’s Whitehall Forest near Athens, Georgia. Diurnal measurements of net C°2 exchange for a mid-summer day in 1988 are presented in Figure 4.

These data suggest that the seedlings had a higher rate of net photosynthesis in the morning than the trees. By mid-afternoon, the rate of net photosynthesis in the trees exceeded that of the seedlings. The lower rates of photosynthesis in the trees were due to lower light levels that occurred in the canopy during the morning hours.

Teskey *et al.* (1986) studied the light response of loblolly pine seedlings (Table 1). These data indicate that light saturation occurred at a PAR levels of greater than 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Higginbotham (1974) developed a similar relationship for the net photosynthetic light response of fifteen-year-old loblolly pine trees grown in the central Piedmont of North Carolina (Table 1). Higginbotham measured the rate of net photosynthesis for three canopy levels at different light intensities in the stand. In these trees, net phototsynthesis continued to increase with increasing PAR up to 2200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. He determined that the rate of net photosynthesis was higher in the middle portion of the canopy than in the upper or lower levels. This response resulted from greater mutual shading in the upper branches caused by a greater leaf area per flush in that part of the crown.

Table 1. Net photosynthesis of seedlings and tree canopy positions of 15 year old *Pinus teada*.

Net CO ₂ exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
PAR	Seedlings	15-year-old tree		
		Upper	Middle	Lower
200	0.63	0.14	0.34	0.64
600	2.52	1.24	1.86	2.10
1000	3.03	1.98	2.71	2.82
1400	3.15	2.42	3.24	3.18
1800	*	2.76	3.57	3.43
2200	*	3.00	3.75	3.56

Note: PAR in $\mu\text{mol m}^{-2} \text{s}^{-1}$
Data from Higginbotham (1974) and Teskey *et al.* (1986)

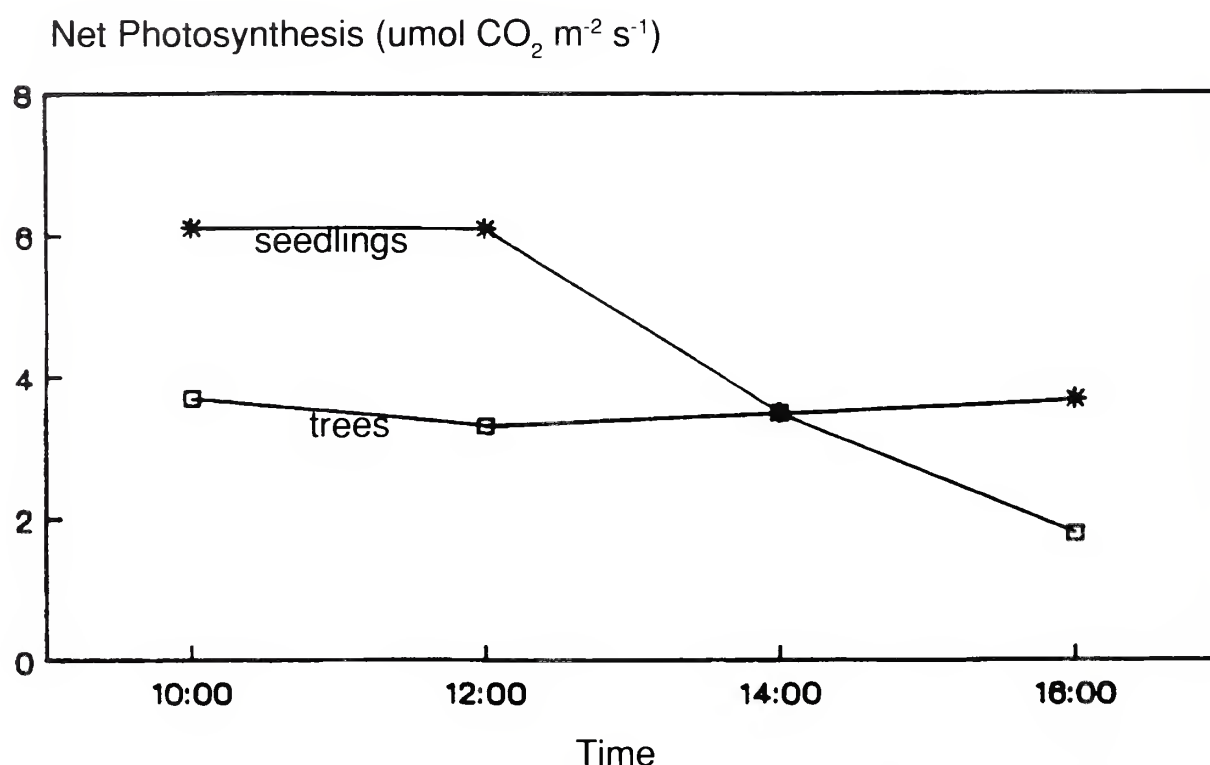


Figure 4. Diurnal pattern of net carbon gain of *Pinus taeda* seedlings and 12-year-old trees from Whitehall Forest, Georgia. Unpublished data from Halpin, 1988.

Water relations

In the summer of 1988, diurnal stomatal conductance measurements were taken concurrently on seedlings and trees at Whitehall Forest, Georgia. The conductance readings for the seedlings at 1000 h were 0.4 cm s^{-1} and declined in a linear fashion to 0.1 cm s^{-1} by 1600 h. The mid-canopy foliage of the trees had conductance readings of 0.15 cm s^{-1} at 1000 h which increased slightly by 1200 h and dropped off by 1600 h to near zero. These data indicate that trees and seedlings can be expected to have different diurnal patterns of water use and carbon gain due to differences in water availability between the shallowly rooted seedlings and deeply rooted trees (Halpin, unpublished).

Another study was performed at the Whitehall Forest to determine how rapidly the seedlings and trees could recharge to their predawn xylem pressure potential values after sunset (Halpin and Cregg, unpublished). Stomatal conductance was measured from late afternoon until stomatal closure occurred. For both trees and seedlings, the conductance read-

ings were zero after sunset. The rate of recharge, however, differed between the seedlings and the trees. By 2100 h, the seedlings had recharged to their predawn xylem pressure potential while the trees did not reach equilibrium until 2400 h. These results emphasize the importance of morphological effects on internal water relations. The faster recovery of the seedlings may be due to several factors, such as more rapid conductance of water flow through the xylem elements and a lower gravitational potential. Also, the simple branch structure of the seedlings allows for relatively easy water movement as compared to the trees in which water must pass through several points of high hydraulic resistance (Ewers and Zimmermann, 1984).

Translocation

As with many of the physiological processes discussed above, the differences in translocation of carbohydrates and growth regulators of seedlings and trees are largely related to differences in anatomy and morphology. Movement of phloem sap has been esti-

mated to range from 100 to 200 cm hour in angiosperms (Salisbury and Ross, 1969). This rate represents nearly instant movement of phloem sap for a seedling less than 1 meter tall. However, assuming an intermediate rate of 150 cm hour⁻¹, carbohydrates produced near the apical shoot of a 50 meter tall *Liriodendron tulipifera* L. would require nearly two days to reach a potential storage site in the roots. Transport rates of growth regulators, such as auxins, may be as low as 0.5 cm hour⁻¹ and, thus, require long periods to move through a large mature tree.

Summary

At the level of physiological processes, seedlings and trees often perform similarly. However, great differences exist in the complexity of their structures and form which may lead to profound differences in the diurnal rates of processes and in their environmental responses. Another notable difference between trees and seedlings is their carbon allocation and use patterns. Mature trees have a significantly higher ratio of respiring to photosynthetic tissue. Carbohydrate reserves also differ between trees and seedlings. These result in changes in the timing and duration of root and shoot growth and differences in their ability to recover from stresses.

Extrapolation of information gathered on seedlings must be cautiously used to interpret tree responses to environmental stresses and direct comparisons must be made carefully. The environments in which the seedlings and trees grow are substantially different due to differences in rooting depth and canopy structure. Trees have the potential to significantly alter their environments (i.e. shade) whereas seedlings do not. Consideration must be given to the process being examined since some will be very similar while others will differ greatly. In general, the more gross the process, the larger the potential for differences to exist between seedlings and trees.

Literature Cited

- Allen, H.L., P.M. Dougherty, and R.G. Campbell. 1988. Manipulation of Water and Nutrients - Practice and Opportunity in Southern U. S. Pine Forests. *Forest Ecology and Management* (in press).
- Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* 28: 355- 377.
- Bormann, F.H. 1956. Ecological implications of changes in the photosynthetic response of *Pinus taeda* seedlings during ontogeny. *Ecology* 37: 70-75.
- Brix, H. 1971. Effects of nitrogen fertilization on photosynthesis and respiration of Douglas-fir. *Forest Science* 17:407-414.
- Ewers, F.W. and M.H. Zimmermann. 1984. The hydraulic architecture of eastern hemlock (*Tsuga canadensis*). *Canadian Journal of Botany* 62(5):940-946.
- Harlow, W.M., E.S. Harrar, and F.M. White. 1979. *Textbook of Dendrology*. McGraw-Hill Book Company, New York, New York, USA.
- Higginbotham, K.O. 1974. The influence of canopy position and the age of leaf tissue on growth and photosynthesis in loblolly pine. PhD. dissertation. Duke Univ. Durham, N.C. USA.
- Knauf, T.A. and M.V. Bilan. 1974. Needle variation on loblolly pine from mesic and xeric seed sources. *Forest Science* 20: 88-90.
- Kramer, P.J. and T.T. Kozlowski. 1979. *Physiology of Woody Plants*. Academic Press, Inc., Orlando, Florida, USA.
- McGinnes, E.A. Jr. 1963. University of Missouri, Agric. Ext. Bull. 841. Columbia, Missouri, USA.
- Panshin, A.J. and C. de Zeeuw. 1980. *Textbook of Wood Technology. 4th edition*. McGraw-Hill Book Company, New York, New York, USA.
- Reich, P.B. and R.G. Amundson. 1985. Ambient levels of ozone reduce net photosynthesis in tree and crop species. *Science* 230:566-570.
- Rook, D.A. and M.J. Carson. 1978. Temperature and irradiance and the total daily photosynthesis of the crown of a *Pinus radiata* tree. *Oecologia* 36:371-782.

- Salisbury, F.B. and C. Ross. 1969. *Plant Physiology*. Wadsworth Publishing Company, Inc., Belmont, California, USA.
- Sands, R. and E.K.S. Nambiar. 1984. Water relations of *Pinus radiata* in competition with weeds. *Canadian Journal of Forest Research* 14:233-237.
- Sasaki, S. and T.T. Kozlowski. 1970. Effect of cotyledon and hypocotyl photosynthesis on growth of young pine seedlings. *New Phytologist* 69: 493-500.
- Sinclair, T.R. and K.R. Knoerr. 1982. Distribution of photosynthetically active radiation in the canopy of a loblolly pine plantation. *Journal of Applied Ecology* 19:183-191.
- Teskey, R.O., J.A. Fites, L.J. Samuelson and B.C. Bongarten. 1986. Stomatal and nonstomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. *Tree Physiology* 2:131-142.
- Thames, J.L. 1963. Needle variation on loblolly pine from four geographic seed sources. *Ecology* 44: 168-169.
- Williams, C.G. 1987. The influence of shoot ontogeny on juvenile-mature correlations in loblolly pine. *Forest Science* 33:411-422.
- Wong, S.C. and F.X. Dunin. 1987. Photosynthesis and transpiration in a eucalypt forest stand: CO₂, light and humidity responses. *Australian Journal of Plant Physiology* 14:619-632.

Mechanisms By Which Regional Air Pollutants Affect Forested Soils and Rhizospheres: The Significance of Long-Term Perspectives

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Introduction

The objective of this paper is to develop a long-term, broadly applicable, and critical perspective about the mechanisms by which regional air pollution alters soil resources. The paper's intention is not to review the literature, but rather to emphasize the necessity for a long-term perspective of soil and ecosystem change, particularly with respect to those causing forest declines. Long-term perspectives are essential to the management of forest ecosystems in areas that are exposed to regional air pollutants.

This paper is organized from the relatively well known to the unknown, and from the relatively simple to the complex. Two examples of forest declines are described initially to suggest the complexity of evaluating how and why ecosystems change. The paper is then divided into three parts to evaluate key mechanisms by which soils are affected by pollution. They are: (1) The changing chemistry, especially the acidification, of the bulk (whole) soil since relatively

good information exists for predicting that the chemistry of most soils changes relatively slowly in response to regional air pollution; (2) The changing chemistry of the soil solution, which is of much greater concern than the gross acidification of whole soils, especially in extremely acid soils. Although supported by chemical theory, relatively little quantitative data exist to document changes in solution chemistry of extremely acidic soils; (3) The changing dynamics of the soil-root system, the rhizosphere, concludes the paper.

Interactive effects of pollutants on soil-root relations are poorly understood yet critical to determining how soil-plant systems respond to air pollutants.

Two Examples of Soil-Mediated Tree Declines

We begin by describing two examples of natural tree declines that are mediated by soil processes. The examples are used to illustrate that soil-mediated stresses of perennial eco-

systems are complex and may be expressed only over the long term. The two examples also demonstrate both the power and the limitations of the scientific mind to understand soil-plant systems.

Decline of *Acacia* in Kenya

In the early 1960's, yellow-fever *Acacia* trees (*A. xanthophloea*) began to die in the savannas at the foot of Mt. Kilimanjaro in the Massai Amboseli Game Reserve. Trees were gradually replaced by sparse grasses and bushes. The forest decline was initially blamed on elephant damage and on overgrazing by Massai herders. A subsequent detailed analysis of climate, soils, hydrology, and historical data (Western and Van Praet, 1973) indicated that high rainfall over several years had elevated saline water tables and increased soluble salts in the root zone. Salt-sensitive *Acacia* trees were replaced by relatively salt-tolerant plants. Because rainfall is markedly cyclic in equatorial Africa, dominant plants in these savanna ecosystems appear to alternate between grasses and trees over decades-long periods.

Western white pine pole blight

In the middle decades of the 20th century, many stands of western white pine in the north-western USA suffered declines associated with root mortality and crown thinning. Causal factors for these physiological stresses were uncertain but symptoms were strongly mediated by soil conditions, e.g., problems were concentrated on sites with shallow, rocky soils (Leaphart and Copeland, 1957). Extrapolating the relation between growth to weather to the long-term tree ring record, Leaphart and Stage (1971) described the years between 1916 and 1940 as having the most adverse growing conditions in the last 300 years. In many stands, the disease persisted for many years following the initial environmental stresses, and growth of many trees that did not die, did not recover from initial stress. In some stands the disease was not

exhibited above-ground for many years following the actual occurrence of stress. These examples demonstrate that perennial forest systems, whether savanna woodland or humid montane forest, require long-term perspective for understanding basic ecosystem dynamics and for implementing management.

The Capacity of Soil Systems: The Changing Chemistry of Bulk Soil

One important reason that dynamics of forest ecosystems are expressed only over the long term is that soil materials buffer and resist chemical change. The capacity concept of soils is used to describe how a soil's solid phase buffers chemical change. Capacity is often contrasted with intensity, a distinction that differentiates elemental content of soil solids (in exchangeable or mineral forms) from the concentration or activity of elements in solution, respectively. The concepts are frequently associated with soil acidity (i.e., exchangeable acidity vs pH), but are also applicable to all elemental species that are distributed in both solid and liquid phases.

In terms of the capacity factors, the most likely effect of acidic deposition is to increase

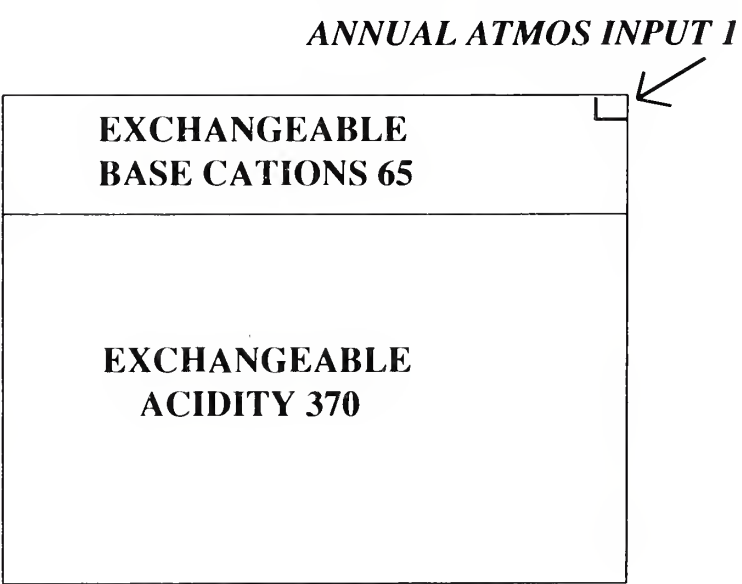


Figure 1. Pool sizes of cations in a relatively poorly buffered soil. Exchangeable cations is shown in relation to 1 kmol/ha/yr, a moderately high input of acid deposition.

exchangeable acidity and to reduce exchangeable base cations (Fig. 1). Figure 1 illustrates the relative pool sizes of exchangeable cations in a poorly buffered soil (after Reuss and Johnson, 1986). In most soils, substantial changes in total exchangeable acidity cannot be expected, except in soils that receive high inputs of acid over many decades. Many soil scientists suggest that acidic deposition affects exchangeable acidity slowly in most soils, due to the soils' capacity to buffer the dilute acid inputs. Despite the range of opinions, it is important to view the capacity of the mineral soil system as relatively resistant to change (Richter, 1986), as is illustrated in Figure 1 based simply on relative pool sizes of soil cations.

Although most soils tend to buffer soil environments, not all soils have large buffer capacities compared to atmospheric inputs. Low activity clays with low cation exchange capacities can be acidified at moderate rates. Such soils are not uncommon in the southeastern USA. An example of the natural acidifica-

tion of a low activity clay soil is described in Table 1 (Wells, 1980). These unique data document how twenty years of pine plantation development reduced base saturation from about 40 to <10% in surface soils. Presumably acidic deposition would have analogous effects on similar soils. Other low buffer capacity soils of concern include extremely acidic soils that contain virtually no exchangeable nutrient cations (Table 2). These acid soils are most common in high elevation humid ecosystems where soil depth restricts rooting volumes. Although not widely distributed, they do support unique and aesthetically valuable forest ecosystems.

The Intensity of Soil Systems:
The Changing Chemistry of Soil Solutions

In terms of intensity factors, the most likely effects of regional air pollution is to alter cation chemistry of soil solutions. In regions downwind from industrialized areas, atmospheric deposition of sulfate has increased electrolytes in soil solutions by 0.1 to 0.5 mM/L over wide

Table 1. Chemical properties of an Appling series Udult at 5, 11, 15, and 20 years after planting of loblolly pine. Letters following numbers in each column indicate significant differences in soils sampled at different ages at p - 0.05 (Wells, 1980).

Stand Age	Carbon	Nitrogen	pHw	Extract P	Exchangeable		
					Ca	Mg	K
yr	%	ug/g	----- ug/g -----				
0 to 7.5 cm depth							
5	0.52a	338a	5.3a	46a	96a	12a	23a
11	0.48ab	280b	5.0b	34b	63b	8b	19b
15	0.44b	234c	4.1c	35b	37c	6c	18b
20	0.46b	229c	3.8d	32b	13d	4d	13c
7.5 to 15 cm depth							
5	0.37a	267a	5.2a	34a	62a	8a	16a
11	0.37a	219b	5.0b	31a	47b	5b	14ab
15	0.37a	190c	4.4c	33a	25c	3c	14ab
20	0.38a	187c	4.3c	32a	22c	3c	11b

Notes: Soil pH was a water paste and extractable P was Bray No.2.

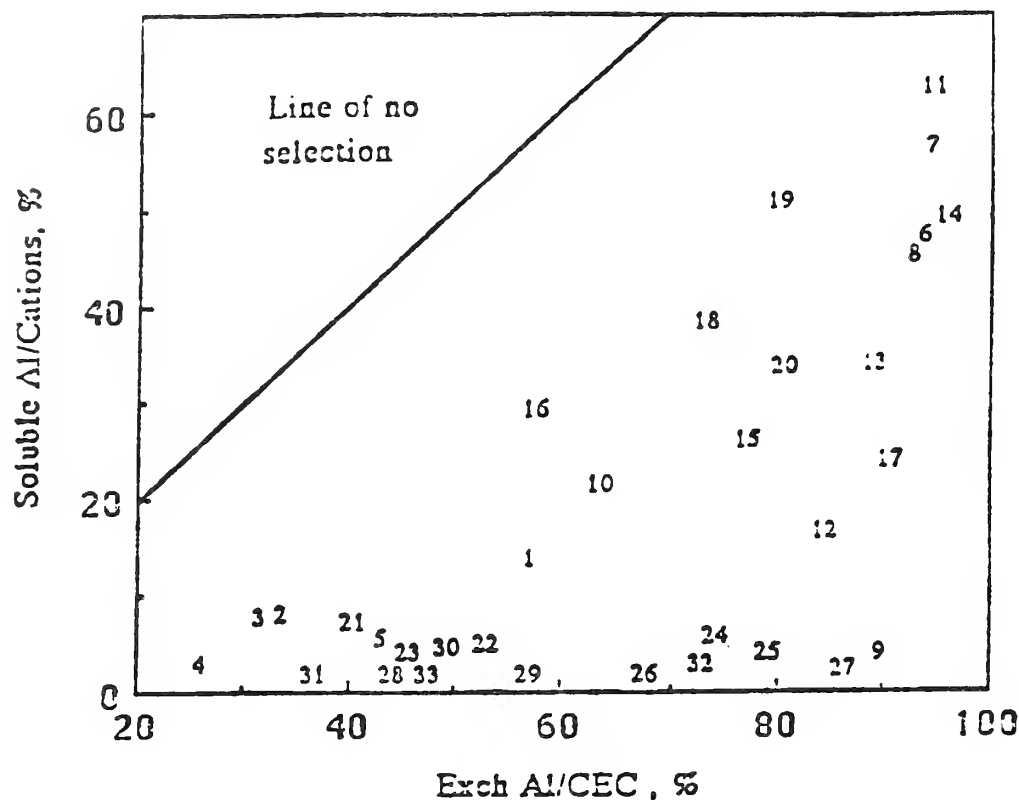


Figure 2. Release of exchangeable Al to soil solution in response to salt (BaCl_2) added at 0.5 meq/L

areas of North America and Europe (Reuss and Johnson, 1983). Depending on a soil's exchange complex, such concentrations may depress pH of soil solutions due to cation exchange reactions and the "salt effect" (Richter *et al.*, 1987). In extremely acidic soils, these increases in electrolytes may substantially elevate aluminum in soil solutions via cation exchange (Dai and Richter, submitted). Data from laboratory simulation of this exchange of aluminum into solution indicates that extremely acidic soils have a marked ability to release aluminum into solution (Fig. 2). Thus, although acidic deposition may not readily acidify acid soils further, it may increase solution concentrations

of aluminum via cation exchange. Short-term concerns over acidic deposition effects should be focused mainly on changes in intensity factors, i.e., soil solution changes, rather than on changes in capacity. One very significant need, for example, is to explain the highly variable aluminum release from extremely acid soils (Fig. 2).

Models are used to predict changes in intensity factors that result from acidic deposition. Many such models are based on theoretical calculations of cation exchange that have little empirical documentation especially at ionic concentrations that are appropriate to field

Table 2. Chemical concentrations and contents of rock-free soil from high elevation (>1500m) spruce-fir stands in the Black Mountains in western North Carolina (Richter *et al.*, submitted).

Statistic	Exchangeable			Total		
	Ca	Mg	K	Ca	Mg	K
Mean, kMc/ha	6.4	3.4	3.0	16.6	336	169
CV, %	38	36	42	47	47	50

Notes: CV % is coefficient of variation of 18 volumetric soil pits 2 in each of 9 stands.

conditions. Figure 2 illustrates a large measure of unexplained soil variation, a variation not accounted for in theoretical models. In contrast, Figure 3 illustrates that different cations, e.g., aluminum and magnesium, are displaced with great predictability from soils that range widely in their chemical properties. Figure 3 also indicates with empirical data that as electrolyte concentrations increase in soil solution (from atmospheric deposition or from natural processes), aluminum is exchanged into solution in greater proportion than any other nutrient cation. However, only in extremely acid soils is aluminum likely to be a dominant cation of soil solutions (Fig. 2). Of course, what is yet to be well understood is the biological significance of these changes in the system's intensity.

The Changing Dynamics of Soil-Root Systems

Tree health is intimately tied to the health of its rhizosphere-root system – that narrow but important continuum linking plant to soil. Roots function as the tree's nutrient and water uptake

and anchoring system, as well as providing protection from soil-borne pathogens, and sequestering of potentially toxic elements. Nutrient availability and root activity are in turn defined by reactions in the rhizosphere. Impacts of pollutants can potentially alter the chemistry and activity of this region by either soil-mediated or plant-mediated means (Table 3). Such change in this soil-plant continuum will have ramifications on nutrient uptake, disease protection, water uptake, and nutrient cycling, and thus on ecosystem stability. Several recent reviews were used in the formulation of this paper and have been listed in the reference section (Anon., 1986; Jansen *et al.*, 1988; Mathy, 1988; NCASI, 1987; Visser *et al.*, 1987).

Understanding the rhizosphere-root subsystem

The rhizosphere is a zone of intense and varied microbial activity ranging from saprophytic to symbiotic to parasitic. Soil nutrient availability and plant uptake are dependent on these activities. The activities interact and fluctuate dramatically in time and space. As

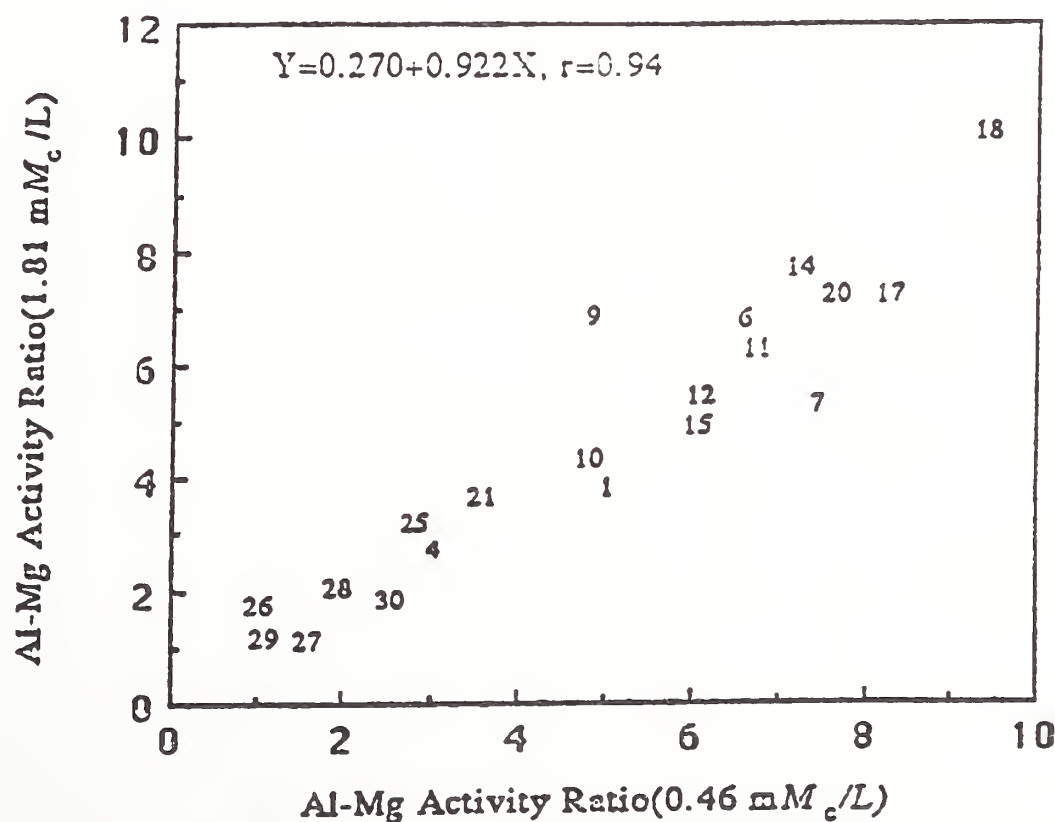


Figure 3. Activity ratios of Al/Mg are relatively constant despite variation in ionic strength of soil solutions

Table 3. Hypothesized mechanisms of atmospheric deposition impact on rhizosphere-root system.

OZONE	ACIDIC DEPOSITION
Carbon partitioning effect on root quantity and quality	Acid, N, and S inputs: increased solubility of potentially toxic elements; increased leaching of nutrients and metals; alteration of nutrient balances.
— Impact within plant without addition of other stresses	
** Alteration of root growth and function	
** Alteration of mycorrhizal formation and function	
** Alteration of nodule formation and function	
— Impact on rhizosphere without addition of other stresses	
** Alteration of quantity and quality of root exudates	
** Alteration of extracellular enzymes, i.e., phosphatases, siderophores	
** Alteration of microbial community structure and function	
— Impact on rhizosphere-root system	
** Alteration on nutrient cycling	
** Alteration on nutrient availability	
** Alteration on nutrient uptake	
** Alteration of buffer/recovery capacity to additional pollutant impact and other stress, i.e., drought and disease	

exposure to atmospheric pollutants may be a temporary, seasonal, or even an infrequent event, the impact to the rhizosphere-root continuum may last only briefly, for most or all of that tree's life or beyond to the next generation of trees. Table 3 lists some of the many hypothesized mechanisms for pollutant impacts on the rhizosphere-root system. Although listed as separate items, each impact feeds back into the others potentially causing further impacts on the system. The multiple interactions that take place in the soil-root continuum make interpretation of impacts difficult. Differences caused by soil type, plant species, plant age, pollutant composition, and exposure dynamics add greatly to the complexity of pollutant interactions. The many studies of this continuum have failed to produce a unified picture of how rhizosphere-root processes such as N mineralization, soil respiration, and mycorrhizal formation and function are affected by atmospheric pollutants.

Advances in understanding the rhizosphere-root subsystem have come from studies that have provided "puzzle pieces" to

the bigger picture. An example of one puzzle piece is work by Zak *et al.* (submitted). Nitrogen uptake by spring ephemeral plants has previously been supposed as the mechanism for N retention in northern hardwood forests prior to overstory N uptake in the early spring. Using ¹⁵N, microbial immobilization was demonstrated to be a more significant sink than plant uptake. Moreover, the strength of this sink was enhanced by the presence of the spring ephemeral plants. Schoeneberger and Perry (1982) found that differences in Douglas-fir growth in two adjacent old growth forested soils was explained by a litter-induced allelopathic reaction that shifted differences in mycorrhizal morpho-types. To understand the impact of pollutants on system performance, many more pieces to the rhizosphere and pollution puzzle need to be evaluated. For example, exposure of subterranean clover, a nitrogen-fixing plant, to a range of ozone concentrations (0 to 0.15 ppm) for 8 weeks, did not affect shoot growth. Root biomass, however, was significantly reduced as ozone increased (Schoeneberger and Shafer, 1987). And, more importantly, increasing ozone was found to reduce the proportion of

nitrogen in the shoot that was derived by symbiotic function, thus altering the plant species composition from one that fixed more N to one that relied more heavily on N mineralized from native soil sources. Such complex interactions of natural systems need to be better appreciated.

The complexity of putting these "puzzle pieces" together to understand the relationships among rhizosphere-root performance, forest decline, and chronic air pollution is also illustrated in a study by Meyer *et al.* (1988). In examining the root and mycorrhizal status of two 30-yr-old *Picea abies* (L.) Karst. stands showing various levels of decline, visual decline symptoms were associated with fewer root and mycorrhizal tips. Significant correlations were found between root numbers and ectomycorrhizal tips per m² ground area and the molar ratio of root calcium to aluminum in mineral soil extracts. Further, a positive relation was found between ectomycorrhizal tips on a per m² leaf area basis and foliar calcium and magnesium contents, and a negative relationship with foliar aluminum content. While these data fit what others have hypothesized as causing forest declines, they can be interpreted in several ways. One hypothesis is that the acidification process at the declining site has resulted in soil conditions (e.g., Ca:Al ratio) that inhibit root and mycorrhizal tip formation which in turn altered the foliar nutrient content. However, it may also be supposed that tip production and foliar nutrient content have both been affected in the same manner but independently from each other by the soil environment.

Conclusions

Currently the majority of pollution studies use short-term, acute dose experimental designs, often in order to meet policy-making deadlines. Whether this approach bears an accurate relationship to current, relatively low-levels, or not, chronic exposures is problematic, especially with regard to the soil-plant contin-

uum. To interpret and predict region-scale atmospheric pollutant effects on soil resources, soil-plant systems, and forest ecosystems, a coordinated team approach with a long-term perspective is necessary.

Literature Cited

- Anonymous. 1986. *Indirect effects of air pollution on forest trees: root-rhizosphere interactions*. Proc., COST Workshop, Julich, FRG. Comm. European Commun., Environ. Res. Prog.
- Dai, K.H., and D.D. Richter. 1989. Ion exchange equilibria involving aluminum in acid forested soils. *Soil Sci. Soc. Am. J.* (submitted).
- Jansen, A.E., J. Dighton, and A.H.M. Bresser. 1988. *Ectomycorrhiza and acid rain*. Proc., Workshop on Ectomycorrhiza/Expert Meeting, Berg en Dal, Bilt-hoven, The Netherlands.
- Leaphart, C.D., and O.L. Copeland, Jr. 1957. Root and soil relationships associated with the pole blight disease of western white pine. *Soil Sci. Soc. Am., Proc.* 21:551-554.
- Leaphart, C.D., and A.R. Stage. 1971. Climate: a factor in the origin of the pole blight disease of *Pinus monticola* Dougl. *Ecology* 52:229-239.
- Mathy, P. (ed.). 1988. *Air pollution and ecosystems*. Reidel Publ. Co., Dordrecht, Holland.
- Meyer, J., B.U. Schneider, K. Werk, R. Oren, and E.-D. Schulze. 1988. Performance of two *Picea abies* (L.) Karst. stands at different stages of decline. V. Root tip and ectomycorrhiza development and their relations to above-ground and soil nutrients. *Oecologia* (in press).
- NCASI. 1987. *Acidic deposition and forest soil biology*. Techn. Bull. 527. New York.
- Reuss, J.O., and D.W. Johnson. 1986. *Acid deposition and the acidification of soils and waters*. Springer-Verlag, New York.
- Richter, D.D. 1986. Sources of acidity in forested Udults. *Soil Sci. Soc. Am. J.* 50:1584-1589.
- Richter, D.D., P.J. Comer, K.S. King, H.S. Sawin, and D.S. Wright. 1987. Effects of low ionic strength solutions on pH of acid forested soils. *Soil Sci. Soc. Am. J.* 52: 261-264.

- Richter, D.D., K.S. King, and J.A. Witter. 1989. Soil nutrient and moisture status in high elevation Umbrepts in the Black Mountains of western North Carolina. *Soil Sci. Soc. Am. J.* (submitted).
- Schoeneberger, M.M., and D.A. Perry. 1982. The effect of soil disturbance on growth and ectomycorrhizae of Douglas fir and western hemlock seedlings: a greenhouse bioassay. *Can. J. For. Res.* 12: 343-353.
- Schoeneberger, M.M., and S.R. Shafer. 1987. Influence of microbial symbionts and ozone on growth and N-fixation of subterranean clover in forest soils. *Am. Soc. Agron. Abstracts*. Atlanta, Ga.
- Visser, S., R.H. Danielson, and J.F. Parr. 1987. Effects of acid-forming emissions on soil microorganisms and microbial-mediated processes. Acid Deposition Res. Prog., Kanaskis Centre for Environ. Res, Univ. Calgary, Canada and USDA Beltsville, MD.
- Wells, C.G. 1980. *Effect of spacing and age on nutrients in needles and soil properties of loblolly pine*. Progress Report. FS-SE-1103-3 (3). USDA Forest Service, Southeastern Forest Exper. Sta., Asheville, NC.
- Western, D., and C. Van Praet. 1973. Cyclical changes in the habitat and climate of an east African ecosystem. *Nature* 241:104-106.
- Zak, D.R., P.H. Groffman, K.S. Pregitzer, S. Christensen, and J. Tiedje. 1989. Plant-microbe competition for inorganic nitrogen. The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. *Ecology* (in review).

Mechanisms of Genetic Control of Air Pollution Tolerance in Forest Trees

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Abstract

The genetic control of air pollution tolerance has been demonstrated in several ways, via grafting, parent-offspring correlations, provenance and family variability studies and heritability estimates. This paper reviews the evidence for genetic control of air pollution tolerance in trees and summarizes the proposed mechanisms for differences in tolerance to the two most thoroughly studied pollutants, sulfur dioxide and ozone.

Introduction

Ecologists studying point source pollution problems were the first to describe genetic variability in air pollution tolerances of forest trees. They noted community changes attributable to natural selection for air pollution tolerance that had occurred in the vicinity of smelters and other large factories. More recently, evidence has been building for regional impacts of air pollution on the genetic structure of forests (Berrang *et al.*, 1986a,b; Kriebel and Leben, 1981; Larsen, 1986; Mejnartowicz, 1983; Miller *et al.*, 1963; Muller-Starck, 1985; Scholz and Bergmann, 1984). The implications of air pollution on the adaptability of forest trees to

other stresses has been discussed by Gregorius (1986). He concluded that "air pollution impairs adaptation of forest tree populations in almost all aspects and fundamentally undermines their natural bases for the preservation of adaptability."

From a practical standpoint, the genetic control of air pollution tolerance means that bio-indicators can be developed with varying responses to air pollution and that tolerant trees can be selected for planting in polluted areas. Trees are useful bio-indicators because of the perennial growth habit, long-term foliar retention (conifers), and minimal culture requirements. While the cleanup of pollution problems at their sources is the best way to alleviate air pollution damage to forest trees, the complex nature of regional air pollution problems suggests that they will continue to be with us well into the next century so that planting tolerant trees is a useful alternative in some situations.

This paper will discuss the studies that have developed the evidence for genetic control of air pollution tolerance in forest trees and will describe proposed mechanisms for this genetic control.

Evidence for genetic control of air pollution tolerance grafting studies

Some of the first evidence for the genetic control of air pollution tolerances of forest trees came from studies where scions of sensitive and tolerant trees were grafted onto rootstock and then transplanted back into areas where air pollution was present. Differential responses of scions and rootstock are evidence of genetic control of air pollution response and are also evidence for an airborne influence rather than a soil-related causal agent. Rohmeder and Schonborn (1965) showed that scions from trees selected for their tolerance to industrial pollutants were less severely injured by sulfur dioxide (SO_2) and hydrogen fluoride (HF) than were scions from trees taken in nonpolluted areas. Similar findings were reported by Dochinger and Seliskar (1965) who utilized grafting studies to show that susceptibility of *Pinus strobus* was genetically controlled. This disease was later found by Dochinger and Seliskar (1970) to be caused by low levels of ozone (O_3) and SO_2 . While grafting provided preliminary evidence of genetic control, it does not indicate whether the trait will be passed on through a sexual generation. Thus, additional lines of evidence were needed.

Provenance, family, and parent-offspring studies

A second type of evidence for genetic control of air pollution tolerance came by comparing the air pollution responses of: (a) various populations from across the range of a species and (b) related individuals as compared to nonrelated individuals in 1/2-sib family, full-sib family or parent-offspring trials. Seed source or provenance differences in the response of trees to ozone has been shown for *Acer rubrum* (Berrang *et al.*, 1986b; Townsend and Dochinger, 1974), *Fraxinus americana* and *F. pennsylvanica* (Karnosky and Steiner, 1981), *Pinus strobus* (Genys and Heggstad, 1983), and *Pinus taeda* (Adams *et al.*, 1988; Kress *et al.*,

1982a,b; Winner *et al.*, 1987), and *Populus tremuloides* Michx. (Berrang *et al.*, 1986a). In all of these studies, a wide range of sensitivity was found following artificial fumigation with O_3 . Similar variability has been reported for response to SO_2 by *Fraxinus americana* and *F. pennsylvanica* (Karnosky and Steiner, 1981), *Picea abies* (Bialobok *et al.*, 1980b; Huttunen, 1978), *Pinus contorta* (Garsed and Rutter, 1982; Lang *et al.*, 1971), *Pinus nigra* (Oleksyn *et al.*, 1987), *Pinus sylvestris* (Huttunen and Tor-malehto, 1982; Karolewski and Pukacki, 1983; Oleksyn and Bialobok, 1986).

The studies mentioned above infer genetic control by describing less variability within families or seed sources than between them. However, it is well known that within seed source and within family variation can also be substantial. This type of variation, often referred to as tree-to-tree variation, can also be genetically controlled although it is more difficult to demonstrate. Clonal propagation is useful in testing variation in tolerance when tree-to-tree variation within seed sources is high, as was the case for *Populus tremuloides* studies by Karnosky (1977) and Wang *et al.* (1986). Heritability estimates are also useful when large amounts of tree-to-tree variation occur.

Parent-progeny correlations are another useful means of demonstrating genetic control of a given trait. Bialobok *et al.* (1978, 1980a) showed that *Pinus sylvestris* progeny of scions tolerant to SO_2 and O_3 were generally more tolerant to these gases than progeny from unselected trees. This same group later reported a high correlation ($r=.639$ and significant at the .01 level) between the degree of SO_2 injury to mother clones and the degree of injury to needles of seedling progenies for *Pinus sylvestris*. The authors concluded from these studies that the heritability of pollution tolerance appears to be high in *Pinus sylvestris*. However, they did not actually calculate heritability estimates.

Heritability estimates

The strongest evidence for genetic control of air pollution tolerances in forest trees comes from studies which estimate heritability which is commonly used in forest genetics because of the long generation times involved with trees. Heritability of air pollution tolerance appears to be very high as estimates from .32 to .80 have been developed for many tree species and for many pollutants (Table 1).

Mechanisms of tolerance

There appear to be a number of mechanisms of air pollution tolerance in forest trees depending on the species and on the pollutant. Mechanisms of tolerance have been most thoroughly studied for SO₂, and O₃. The discussion will address these two pollutants.

Sulfur dioxide

Differential depression of photosynthesis by SO₂ has been reported for sensitive and tolerant trees of *Pinus strobus* (Eckert and

Houston, 1980), *Pinus sylvestris* (Oleksyn, 1981), and *Abies alba* (Larsen *et al.*, 1988). The reduction in photosynthesis in sensitive clones was about six times greater than in tolerant clones. Thus, the complex photosynthetic apparatus, including stomates, enzymes, chlorophyll and/or chloroplasts, may be more sensitive to SO₂ exposure in some sensitive genotypes. Another proposed mechanism for the increased sensitivity of some genotypes to SO₂ is that some sensitive trees are more photosynthetically active and so thereby take in more CO₂. Assimilating more CO₂, these individuals may at the same time absorb and assimilate larger quantities of SO₂, and as a consequence, be injured to a greater degree by this gas as has been reported by Jensen and Kozlowski (1975), Lorenc-Plucinska (1978a,b, 1982), Oleksyn (1981), and Oleksyn and Bialobok (1986). Kimmerer and Kozlowski (1981) found leaf stomatal conductance to be an important factor in determining the relative sensitivity of *Populus tremuloides* clones to SO₂. They suggested that stomatal closure may occur in some tolerant *Populus* clones while other tolerant clones keep their stomates open in the presence of SO₂ and

Table 1. Heritability estimates for air pollution tolerance in forest trees.

Species	Pollutant	Heritability Calculation	Heritability Estimate	Reference
<i>Picea abies</i>	HF	h^2_{BS}	.60	Scholz <i>et al.</i> , 1979
<i>Picea</i> species	SO ₂	h^2_{NS}	.60	Tzchacksch, 1981
<i>Pinus strobus</i>	SO ₂ + O ₃	r	.80	Houston & Stairs, 1973
<i>Pinus strobus</i>	SO ₂	h^2_{BS}	.32 to .64	Thor & Gall, 1976
<i>Pinus sylvestris</i>	SO ₂	h^2_{NS}	.60	Tzchacksch, 1982
<i>Populus tremuloides</i>	O ₃	r	.62	Karnosky, 1977
<i>Populus tremuloides</i>	SO ₂	r	.64	Karnosky, 1977
<i>Pseudotsuga menziessi</i>	SO ₂	h^2_{NS}	.60	Tzchacksch, 1982

¹r = repeatability; h^2_{BS} = broad sense heritability; h^2_{NS} = narrow sense heritability.

somehow appear to be able to detoxify the gas.

Higher levels of the reducing sugars glucose and fructose in SO_2 -sensitive conifer needles than in needles from tolerant trees are presumed to be evidence for another mechanism of differential tolerance. This mechanism is associated with disturbance in translocation of newly produced photosynthate. Evidence for this mechanism of tolerance has been shown for *Pinus sylvestris* (Lorenc-Plucinska, 1984, 1986; Mejnartowicz and Lukasiak, 1985), *Pinus strobus* (McLaughlin *et al.*, 1982), and *Pinus banksiana* (Malhotra and Sarkar, 1979).

Schindlbeck (1977) found that SO_2 -resistant *Picea abies* clones did not have increased glutathione levels after fumigation with SO_2 , while sensitive ones did. Bortitz (1969) and Braun (1977a,b,c) found that the pH of the cell sap in needles of resistant *Picea abies* trees was higher than in sensitive trees. Other researchers have found a good correlation between buffering capacity and resistance (Grill and Hartel, 1972; Scholz and Knabe, 1976) in *Picea*. Similar correlations have been found between SO_2 tolerance and drought-stress tolerance (Braun, 1978) and between SO_2 tolerance and winter hardiness (Huttunen, 1978; Huttunen and Tormalahto, 1982).

Differences in foliar peroxidase levels between SO_2 -tolerant and sensitive trees have been reported for *Pinus sylvestris* (Kieliszewska-Rokicka, 1979) and *Pinus strobus* (Eckert and Houston, 1982). While peroxidase enzymes are a general stress response, other enzyme systems may be more directly related to SO_2 sensitivity. Geburek *et al.* (1987) found evidence indicating that glutamate dehydrogenase and glutamate oxaloacetate transaminase may be involved in SO_2 -sensitivity responses in *Pinus sylvestris*.

Ozone

Two types of mechanisms for O_3 toler-

ances of trees have been reported: anatomical and physiological. Evans and Miller (1972) presented evidence that needle anatomy may contribute to differences in O_3 tolerance with four *Pinus* species. The secondary leaves of the more ozone-sensitive species had a larger number of stomata per cross-sectional area of mesophyll cells while the number of mesophyll cells per stoma was lower. The number of hypodermal layers and thickness of epidermal and hypodermal layers were negatively correlated with ozone sensitivity. In our laboratory, we found that there was no relationship of stomate number per given leaf area and O_3 sensitivity for *Fraxinus pennsylvanica* and *Populus tremuloides* (Rassatt *et al.*, unpublished). However, for *F. pennsylvanica*, we did find that the proportion of the spongy mesophyll region relative to all mesophyll was greater for sensitive trees than for tolerant trees. Since this spongy mesophyll region contains a great deal of intercellular space, it appeared that O_3 would have more exposed cell surface to react with in the sensitive trees.

Evans and Miller (1972) suggested that there was a higher mesophyll tissue resistance which limits gas exchange in more tolerant pine trees. Our results suggest that a similar mechanism may occur in green ash trees.

Another anatomical feature that may influence O_3 sensitivity in *Pinus strobus* is needle wax. Krause and Houston (1982) reported that the epistomatal wax was split longitudinally across the stomatal apertures in 13 sensitive clones, but was continuous in the 11 tolerant clones examined. This character was apparent for ramets grown in either ambient or clean air. Trimble *et al.* (1982) did not find differences in wax structure of a sensitive and a tolerant clone of *Pinus strobus*. However, the alkane concentration was greater in the wax of the tolerant clone.

Evidence for physiological mechanisms of tolerance generally center on the uptake of

gases through the stomates. Reich (1987) believes that among species, differences in ozone uptake and response can be predicted from differences in the inherent leaf diffusive conductance. There has not been enough study of leaf diffusive conductance comparing within species differences in O_3 tolerance to determine if this mechanism also is important in intraspecific variation in pollution tolerance.

Boyer *et al.* (1986) found another physiological mechanism of tolerance in *Pinus strobus*. Ozone consistently depressed photosynthesis in sensitive clones more than in tolerant clones. Differences in growth rates between sensitive and tolerant *Populus tremuloides* clones has been documented in field trials under ambient O_3 by Berrang *et al.* (1988) and in chamber tests under various O_3 exposures by Keller (1988). Keller noted that the sensitive trees lost their leaves prematurely in the presence of O_3 and had less carbohydrate reserves as determined by shoot dry weights. He emphasized the importance of multiple-year studies for evaluating growth differences in response to O_3 .

Summary

There appears to be a number of different types of mechanisms involved in differential responses to air pollution by forest trees. Several anatomical features and physiological responses have been shown to vary between sensitive and tolerant trees, with the most common pollutants SO_2 and O_3 . Little is known, however, regarding the biochemical bases for the tolerance mechanisms, and even less is known about the numbers of genes and types of gene action involved in determining pollution sensitivity. Thus, considerable research remains to be done in this field.

Literature Cited

- Adams, M.B., J.M. Kelly, and N.T. Edwards. 1988. Growth of *Pinus taeda* L. seedlings varies with family and ozone exposure level. Water, Air and Soil Pollution (In Press).
- Berrang, P., D.F. Karnosky, R.A. Mickler, and J.P. Bennett. 1986a. Natural selection for ozone tolerance in *Populus tremuloides*. *Can. J. For. Res.* 16:1214-1216.
- Berrang, P., D.F. Karnosky, R.A. Mickler, and J.P. Bennett. 1986b. Population changes in eastern hardwoods caused by air pollution. *Proc. North. American Forest Biol. Workshop.* pp. 3-10.
- Berrang, P., D.F. Karnosky, and J.P. Bennett. 1988. Natural selection for ozone tolerance in *Populus tremuloides*: Field verification of chamber fumigation data. (Manuscript in Preparation.)
- Bialobok, S., P. Karolewski, and L. Rachwal. 1978. Charakterystyka urzadn sluzacych do badania wplywu szkodliwych gazow na rosliny. *Arbor. Korn.* 23:239-249.
- Bialobek, S., P. Karolewski, and J. Oleksyn. 1980a. Sensitivity of Scots pine needles from mother trees and their progenies to the action of SO_2 , O_3 , a mixture of these gases, NO_2 and HF. *Arbor. Korn.* 25:289-303.
- Bialobok, S., J. Oleksyn, and P. Karolewski. 1980b. Differentiation in sensitivity of six Polish provenances of Norway spruce (*Picea abies* (L.) Karst.) to sulphur dioxide. *Arbor. Korn.* 25:305-310.
- Bortitz, S. 1969. Physiologische und biochemische Beitrage zur Rauch schaden forschung. II. Mitteilung: Analysen einiger Nadelinhalts- stoffe an Fichten unterseidlicher individueller Rauchharte aus einem Schadgebiet. *Arch. Forstwes.* 18(2):123-131.
- Boyer, J.N., D.B. Houston, and K.F. Jensen. 1986. Impacts of chronic SO_2 , O_3 and $SO_2 + O_3$ exposures on photosynthesis of *Pinus strobus* clones. *Eur. J. For. Path.* 16:293-299.
- Braun, G. 1977a. Uber die Urachen und Kriterien der Immissionsresistenz bei Fichte, *Picea abies* (L.) Karst. I. Morphologische-anatomische Immissionsresistenz. *Eur. J. For. Path.* 7:23-24.

- Braun, G. 1977b. Über die Ursachen und Kriterien der Immissionsresistenz bei Fichte, *Picea abies* (L.) Karst. II. Reflektorische Immissionsresistenz. *Eur. J. For. Path.* 7:129-152.
- Braun, G. 1977c. Über die Ursachen und Kriterien der Immissionsresistenz bei Fichte, *Picea abies* (L.) Karst. III. Schadstoffverträglichkeit ("innere Resistenz"). *Eur. J. For. Path.* 7:236-249.
- Braun, G. 1978. Über die Ursachen und Kriterien der Immissionsresistenz bei Fichte, *Picea abies* (L.) Karst. IV. Erholungsfähigkeit der Nadeln, Wechselwirkungen zwischen den Resistenzformen und zusammenfassendes Gesamtergebnis. *Eur. J. For. Path.* 8:83-96.
- Dochinger, L.S., and C.E. Seliskar. 1965. Results from grafting chlorotic dwarf and healthy eastern white pine. *Phytopathology* 55:404-407.
- Dochinger, L.S., and C.E. Seliskar. 1970. Air pollution and the chlorotic dwarf disease of eastern white pine. *For. Sci.* 16:46-55.
- Eckert, R.T., and D.B. Houston. 1980. Photosynthesis and needle elongation response of *Pinus strobus* clones to low-level sulfur dioxide exposures. *Can. J. For. Res.* 10:357-361.
- Eckert, R.T., and D.B. Houston. 1982. Foliar peroxidase and acid phosphate activity response to low-level SO₂ exposure in eastern white pine clones. *Forest Sci.* 28:661-664.
- Evans, L.S., and P.R. Miller. 1972. Comparative needle anatomy and relative ozone sensitivity of four pine species. *Can. J. Bot.* 1067-1071.
- Garsed, S.G., and A.J. Rutter. 1982. Relative performance of conifer population in various tests for sensitivity to SO₂, and the implications for selecting trees for planting in polluted areas. *New Phytol.* 92:349-367.
- Geburek, T., F. Scholz, W. Knabe, and A. Vornweg. 1987. Genetic studies by isozyme gene loci on tolerance and sensitivity in an air-polluted *Pinus sylvestris* field trial. *Silvae Gen.* 36:49-53.
- Genys, J.B., and H.E. Heggestad. 1983. Relative sensitivity of various types of eastern white pine, *Pinus strobus*, to sulfur dioxide. *Can. J. For. Res.* 13:1262-1265.
- Gregorius, H.-R. 1986. The importance of genetic multiplicity for tolerance of atmospheric pollution. Proc. 18th IUFRO World Congress, Ljubljana Div. 2, 1:295-305.
- Grill, D., and O. Hartel. 1972. Zellphysiologische und biochemische Untersuchungen an SO₂-belasteten Fichtennadeln. Resistenz und Pufferkapazität. *Mitt. Forstl. Vers.-Anst.* 97:367-386.
- Houston, D.B., and G.R. Stairs. 1973. Genetic control of sulfur dioxide and ozone tolerance in eastern white pine. *For. Sci.* 19:267-271.
- Huttunen, S. 1978. The effects of air pollution on provenances of Scots pine and Norway spruce in northern Finland. *Silva Fennica* 12:1-16.
- Huttunen, S., and H. Tormalaht. 1982. Air pollution resistance of some Finnish *Pinus sylvestris* L. provenances. *Aquilo Ser. Bot.* 18:1-19.
- Jensen, K.F., and T.T. Kozlowski. 1975. Absorption and translocation of sulphur dioxide by seedlings of four forest tree species. *J. Environ. Qual.* 4:379-382.
- Karnosky, D.F. 1976. Threshold levels for foliar injury to *Populus tremuloides* by sulfur dioxide and ozone. *Can. J. For. Res.* 6:166-169.
- Karnosky, D.F. 1977. Evidence for genetic control of response to sulphur dioxide and ozone in *Populus tremuloides*. *Can. J. For. Res.* 7:437-440.
- Karnosky, D.F., and K.C. Steiner. 1981. Provenance and family variation in response of *Fraxinus americana* and *F. pennsylvanica* to ozone and sulfur dioxide. *Phytopathology* 71:804-807.
- Karolewski, P., and P. Pukacki. 1983. Sensitivity of Polish races of Norway spruce (*Picea abies* (L.) Karst.) to the action of sulphur dioxide and low temperatures. *Arbor. Korn.* 28:129-136.
- Keller, T. 1988. Growth and premature leaf fall in American aspen as bio-indications for ozone. *Environ. Pollut.* 52:183-192.
- Kieliszewska-Rokicka, B. 1979. Peroxidase activity in varieties of Weigela and *Pinus sylvestris* resistant and susceptible to SO₂. *Arbor. Korn.* 24:313-320.
- Kimmerer, T.W., and T.T. Kozlowski. 1981. Stomatal conductance and sulfur uptake of five clones of *Populus tremuloides* exposed to sulfur dioxide. *Plant Physiol.* 67:990-995.

- Krause, C.R., and D.B. Houston. 1983. Morphological variation in epicuticular wax of SO₂-sensitive and -tolerant eastern white pine clones. *Phytopathology* 73:1266-1269.
- Kress, L.W., J.M. Skelly, and K.H. Hinkelmann. 1982a. Relative sensitivity of 18 full-sib families of *Pinus taeda* to O₃. *Can. J. For. Res.* 12:203-209.
- Kress, L.W., J.M. Skelly, and K.H. Hinkleman. 1982b. Growth impact of O₃, NO₂, and/or SO₃ on *Pinus taeda*. *Environ. Mon. Assess.* 1:229-239.
- Kriebel, H.B., and C. Leben. 1981. The impact of air pollution on the gene pool of eastern white pine. *XVII IUFRO World Congress. Kyoto, Japan. Proc. Div. 2*, pp. 185-189.
- Lang, K.J., P. Neumann, and P. Schutt. 1971. The effect of seed-source and fertilizing on SO₂-sensitivity of *Pinus contorta* seedlings. *Flora* 160:1-9.
- Larsen, J.B. 1986. Das Tannensterben: Eine neue Hypothese zur Klarung des Hintergrundes dieser ratselhaften Komplexkrankheit der Weissstanne *Abies alba* Mill.). *Forstwissenschaftliches Centralblatt* 105:381-396.
- Larsen, J.B., X.M. Qian, F. Scholz, and I. Wagner. 1988. Ecophysiological reactions of different provenances of European silver fir (*Abies alba* Mill.) to SO₂ exposure during winter. *Eur. J. For. Path.* 18: 44-50 .
- Lorenc-Plucinska, G. 1978a. The effect of SO₂ on photosynthesis and dark respiration of larch and pine differing in resistance to this gas. *Arbor. Korn.* 23:121-132.
- Lorenc-Plucinska, G. 1978b. Effect of sulphur dioxide on photosynthesis, photorespiration and dark respiration of Scots pine differing in resistance to this gas. *Arbor. Korn.* 23:133-144.
- Lorenc-Plucinska, G. 1982. Effect of sulfur dioxide on CO₂ exchange in SO₂-susceptible Scots pine seedlings. *Photosynthetica* 16:140-144.
- Lorenc-Plucinska, G. 1984. The uptake and translocation of ¹⁴C in Scots pine seedlings of differing susceptibility to sulphur dioxide. *Eur. J. For. Path.* 14:310-318.
- Lorenc-Plucinska, G. 1986. Effect of sulphur dioxide on the partitioning of assimilates in Scots pine (*Pinus sylvestris* L.) seedlings of different susceptibility to this gas. *Eur. J. Forest Path.* 16:266-273.
- Malhotra, S.S., and S.K. Sarkar. 1979. Effects of sulphur dioxide on sugar and free amino acid content of pine seedlings. *Physiol. Plant.* 47:223-228.
- McLaughlin, S.B., R.K. McConathy, D. Duvik, and L.K. Mann. 1982. Effects of chronic air pollution stress on photosynthesis, carbon allocation, and growth of white pine trees. *For. Sci.* 28:60-70.
- Mejnartowicz, L.E. 1983. Changes in genetic structure of Scots pine (*Pinus sylvestris* L.) population affected by industrial emission of fluoride and sulphur dioxide. *Genetica Pollonica* 24:41-47.
- Mejnartowicz, L.E., and H. Lukasiak. 1985. Level of sugars in Scots pine trees of different sensitivity to fluoride and sulphur dioxide. *Eur. J. For. Path.* 15:193-198.
- Miller, P.R., J.R. Parmeter, Jr., O.C. Taylor, E.A. Cardiff. 1963. Ozone injury to the foliage of ponderosa pine. *Phytopathology* 53:1072-1076.
- Muller-Starck, G. 1985. Genetic differences between tolerant and "sensitive" beeches (*Fagus sylvatica* L.) in an environmentally stressed adult forest stand. *Silvae Genet.* 34:241-247.
- Oleksyn, J. 1981. Effect of sulphur dioxide on net photosynthesis and dark respiration of Scots pine individuals differing in susceptibility to this gas. *Arch. Ochron. Srod.* 4:49-58.
- Oleksyn, J., and S. Bialobok. 1986. Net photosynthesis, dark respiration and susceptibility to air pollution of 20 European provenances of Scots pine (*Pinus sylvestris* L.). *Environ. Pollut. (Series A)* 40:287-302.
- Oleksyn, J., K. Oleksynowa, E. Kozłowska, and L. Rachwal. 1987. Mineral content and the sensitivity of black pine (*Pinus nigra*) of various provenances to industrial air pollution. *Forest Ecology and Management* 21:237-247.
- Reich, P.B. 1987. Quantifying plant response to ozone: A unifying theory. *Tree Physiology* 3:63-91.
- Rohmeder, E., and U.A. Schonborn. 1965. Der Einfluss von Umwelt und Erbgut auf die Widerstandsfähigkeit der Waldbaume gegenüber Luftverunreinigung durch Industrieabgase. *Forstw. Zentbl.* 84:1-13.
- Schindleck, W.E. 1977. Biochemische Beiträge zur Immissionsforschung. *Forstwiss. Zentbl.* 96:67-71.

- Scholz, F., and F. Bergmann. 1984. Selection pressure by air pollution as studied by isozyme-gene-systems in Norway spruce exposed to sulphur dioxide. *Silvae Genetica* 33:238-240.
- Scholz, F., and W. Knabe. 1976. Investigations on buffering capacity in spruce clones of different resistance to air pollution. In: *XVI IUFRO World Congress. Oslo*. Section S 2.09.04 6 pp.
- Scholz, F., T. Timman, and D. Krusche. 1979. Untersuchungen zur Variation der Resistenz gegen HF-Begasung bei *Picea abies* Familien. *Proc. IUFRO Meeting S2,09-00 (1978) Mitteilungen des Instituts für Forst- und Holzwirtschaft Ljubljana*. pp. 249-258.
- Thor, E., and W.R. Gall. 1976. Variation in air pollution tolerance and growth rate among progenies of southern Appalachian white pine. *Proc. First Conf. Metropolitan Tree Improv. Alliance. Lanham, Md.* pp. 80-86.
- Townsend, A.M., and L.S. Dochinger. 1974. Relationship of seed source and developmental stages to the ozone tolerance of *Acer rubrum* seedlings. *Atmos. Environ.* 8:957-964.
- Trimble, J.L., J.M. Skelly, S.A. Tolin, and D.M. Orcutt. 1982. Chemical and structural characterization of the needle epicuticular wax of two clones of *Pinus strobus* differing in sensitivity to ozone. *Phytopathology* 72:652-656.
- Tzschacksch, O. 1981. Stand und Perspektiven der forstlichen Rauchresistenz-zucht in der DDR. *Beiträge f.d. Forstwirtschaft*. 15:134-137.
- Tzschacksch, O. 1982. Untersuchungen zur Erbllichkeit der SO₂-Resistenz bei Kiefer (*Pinus sylvestris* L.) und Douglasie (*Pseudotsuga menziesii* (Mirb/Franco)) mit Schlussfolgerungen für die Forstwirtschaft. *Beiträge f.d. Forstwirtschaft*. 16:103-106.
- Wang, D., D.F. Karnosky, and F.H. Bormann. 1986. Effects of ambient ozone on the productivity of *Populus tremuloides* Michx. grown under field conditions. *Can. J. For. Res.* 16:47-55.
- Winner, W.E., I.S. Cotter, H.R. Powers, Jr., and J.M. Skelly. 1987. Screening loblolly pine seedling responses to SO₂ and O₃: Analysis of families differing in resistance to fusiform rust disease. *Environ. Pollut.* 47:205-220.

Forest Health Diagnosis and Its Application in Air Pollution Impact Studies

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Introduction

In developing and monitoring strategies for forest management, there is a need to define the health of the basic component of the forest ecosystem — the tree stand. The long distance transport of pollutants, including widely spread regional pollution, contribute to this need for methods for diagnosing forest health.

There have been many studies on diagnosing damage from air pollution. Descriptions of leaf injury from one pollutant or another are often accompanied by color photographs that provide a better understanding of the peculiarities of chlorosis and necrosis and the nature of the pollutant in question (Env. Prot. Agency, 1978; Malhotra and Blauel, 1980; Skelly *et al.*, 1987).

For the grasses, especially annuals, leaf damage is both an adequate characterization of a plant's condition at a given moment and a reliable indicator of future health. For trees, however, this is not the case. For example, leaf damage or even complete defoliation of deciduous trees in the second half of growing season has little influence on tree condition the following year. Therefore, tree-damage scales based

only on foliage condition (for instance, the IUFRO scale) have slight predictive value. As a rule, damage scales are expressed numerically, for example, 0 to 4 (Dassler, 1981) or 1 to 6 (U.S.S.R. State Comm. of For. Manage., 1970). In the latter scale, trees are rated as: healthy (1), weakened (2), heavily weakened (3), dying (4), recently dead (up to 1 year after death) (5); or standing dead (1 year +) (6).

Due to their arbitrary and artificial nature, numerical damage scales have been criticized in the literature (Alexeyev, 1982; Muir and McCune, 1987; Reuther, 1987). Therefore, the first task in developing a diagnostic system is (1) strengthening the reliability of criteria for evaluating tree health, and (2) shifting from numerical indices to their common sense meaning.

The next task is concerned with the method of calculating the life condition (health) of tree stands. This usually is done by the number of trees method, that is, multiplying the corresponding index by the number of trees in that condition, summarizing the values obtained and dividing the total by the total number of trees. However, the use of this method can produce errors because the role of large and small trees

are assigned similar values.

The objective of this paper was to develop a method of diagnosing forest health and to demonstrate its use in a study of northern forests of the U.S.S.R. affected by air pollution.

Diagnosing Tree Health

The proposed categories of tree health are based on characteristics of the tree crown. The scale can be used both for forests damaged by any type of stress (including air pollution) and undamaged forests. The resulting information is not intended to indicate the causes of one or another condition of the tree — for this, a listing of additional specific indicators used by phytopathologists would be necessary in each situation.

Tree Health Scale

Healthy. There are no apparent signs of crown or stem disturbance. Crown density is typical of that of dominant trees (I-II Classes of Kraft's classification, if applicable). Dead and drying branches are observed mostly in the lower part of the crown; in the upper crown, there are no large dead branches or they are too few to be seen in the crown edges. Fully developed leaves and needles are green or dark green. Needle life is typical of that in the region. Leaf damage is negligible (less than 10 percent) and does not affect the state of the whole tree.

Weakened (damaged)¹. At least one of the following must be observed: a) crown density is decreased by 30 percent due to premature shedding of leaves or thinning of the crown frame; b) dead and/or drying branches account for 30 percent of the upper crown; c) 30 to 40 percent total leaf area is damaged (fire, insects, air pollution, or other agents) and no longer participates in photosynthetic activity.

In this category, there may be trees with one or more of these features (or parts of them) and other disturbances (including stem and root damage), with a cumulative effect of weakening equal to 30 percent.

Heavily weakened (heavily damaged).

At least one of the following must be observed: a) crown density is reduced by 60 percent due to premature shedding of leaves or thinning of the crown frame; b) dead and/or drying branches account for 60 percent of the upper crown; c) 60 percent of the total leaf area is damaged (fire, insects, air pollution, or other agents) and no longer participates in photosynthetic activity.

In this category, there may be trees with one or more of these features (or parts of them) and other disturbances (including stem and root damage), with a cumulative effect of weakening equal to 60 percent.

Dying. The primary signs of dying (drying) are: a) the crown is destroyed, its density being 20 percent (or less) of that of a healthy tree; b) more than 70 percent of the branches in the upper crown are dry or drying. The remaining leaves are chlorotic and necrotic.

Dead. There are no living twigs. In the first year after death, the tree has some residual dry needles or leaves. Gradually the twigs, branches, and bark fall off.

As stated earlier, the defoliation of deciduous species or summer-green coniferous species indicates the current state of individual trees, but does not always affect their health the following year. For conifers, the influence of needle damage (premature shedding) is long term because quantitative and qualitative regeneration of the photosynthetic part of a tree takes at least 3 years.

The state of the upper twigs and branches

¹Since tree decline often is related to damage of the photosynthetic system, hereafter "weakened" trees also are considered as "damaged."

of the crown is the most informative for predicting tree health. Healthy, dying, or dead trees usually are easily identified. The external appearance of weakened and heavily weakened trees also is easily distinguished so long as their condition is near the "center" of the gradation being used. A tree whose condition does not fall into a specific category can be recorded as intermediate or related to the most representative category.

The optimal time for inspecting stands is the beginning of the second half of the growing season when the majority of species have finished putting forth leaves and shoots.

Calculating Stand Health

After the condition of the trees on the site plots is determined, the value of a whole stand's health is calculated. For this purpose, coefficients are assigned to trees corresponding to their vitality level. Healthy trees are assigned a coefficient of 100 percent; dead trees receive a coefficient of 0 percent. For trees in intermediate stages, the coefficients of vitality correspond to the health ratings that were assigned during the inventory. In principle, vitality coefficients may be assigned to each tree on a fractional basis. However, because a tree's exterior varies due to its genetics, the accuracy of health ratings is low (usually no more than 10 percent). For trees in the intermediate category, it is reasonable to assume that weakened trees have 70 percent potential vitality, heavily weakened trees, 40 percent, and dying trees, 5 percent.

The estimate for stand health is derived from:

$$L_v = \frac{100v_1 + 70v_2 + 40v_3 + 5v_4}{V}$$

where L_v is relative to the stand vitality in relation to tree volume; v_1 is the stem volume of healthy

(100 percent) trees ($\text{m}^3 \text{ ha}^{-1}$); v_2 , v_3 , and v_4 , are stem volumes for weakened (70 percent), heavily weakened (40 percent), and dying (5 percent) trees, respectively, and V is total stand volume, including standing dead trees ($\text{m}^3 \text{ ha}^{-1}$).

At an L_v of 80 to 100 percent, stand vitality is considered "healthy" ($L_v = 80$ to 90 percent at the onset of weakening); at an L_v of 50 to 79 percent, the stand is considered weakened, at an L_v of 20 to 49 percent, the stand is defined as heavily weakened, and at an L_v of 19 percent or less, the stand is assumed to be destroyed.

Calculations of stand vitality based on the number of trees are simple and efficient compared to those based on the additional consideration of timber volume; however, the "number of trees" method is less accurate because it assigns the same value to trees of different size and function.

Both methods reach the same conclusion if applied to stands without naturally suppressed trees (for example, under regular thinnings). For overstocked pole stands with many small, depressed trees, the "number of trees" method produces large errors. However, in deciding special problems, estimating the health of managed stands (parks), for instance, the "number of trees" method is the only appropriate application.

Air pollution and the Forests of the Northern Kola Peninsula

In 1978-88, as part of the IUFRO 02.03-21 Project (Alexeyev and Dochinger, 1981), the impact of air pollution on the composition, structure, and productivity of forests was studied. The field research was carried out in various regions of the U.S.S.R., primarily in the northern forest ecosystems of Kola Peninsula near the active copper-nickel smelter "Severonikel." Daily emissions from the smelter total 800 to 900 tons of sulphur dioxide with an admixture of trace metals (Cu, Ni, Co).

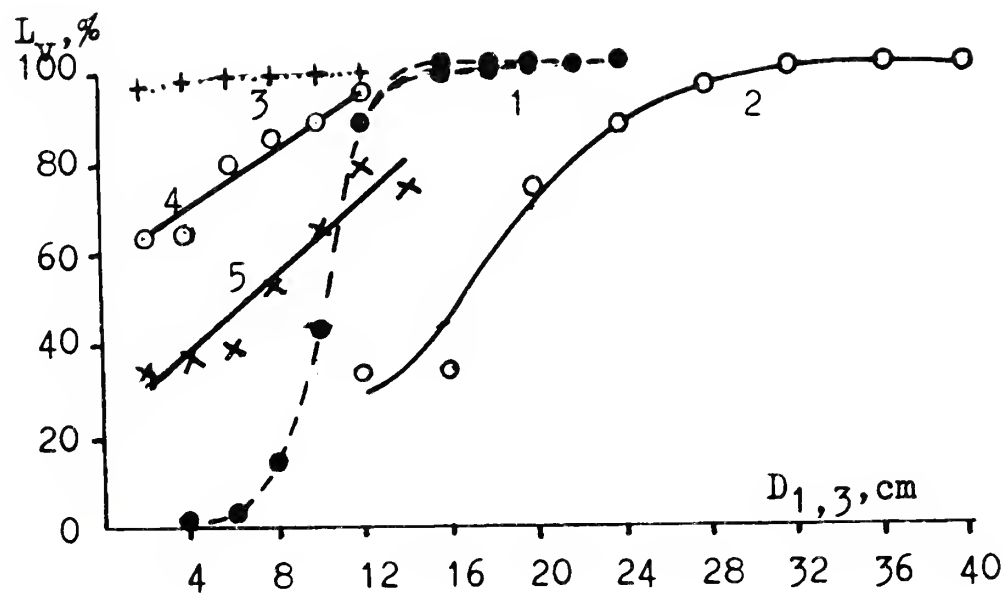


Figure 1. Effect of air pollution on Scotch pine stands in the U.S.S.R. (1) overstocked pole stand in southern taiga, no pollution; (2) fully stocked mature stand in southern taiga, no pollution; (3) understocked, sparse pole stand in northern taiga, no pollution; (4) 27 year old pole stand in northern taiga, 50 percent canopy density due to effects from copper-nickel smelter; (5) the same site in 1988.

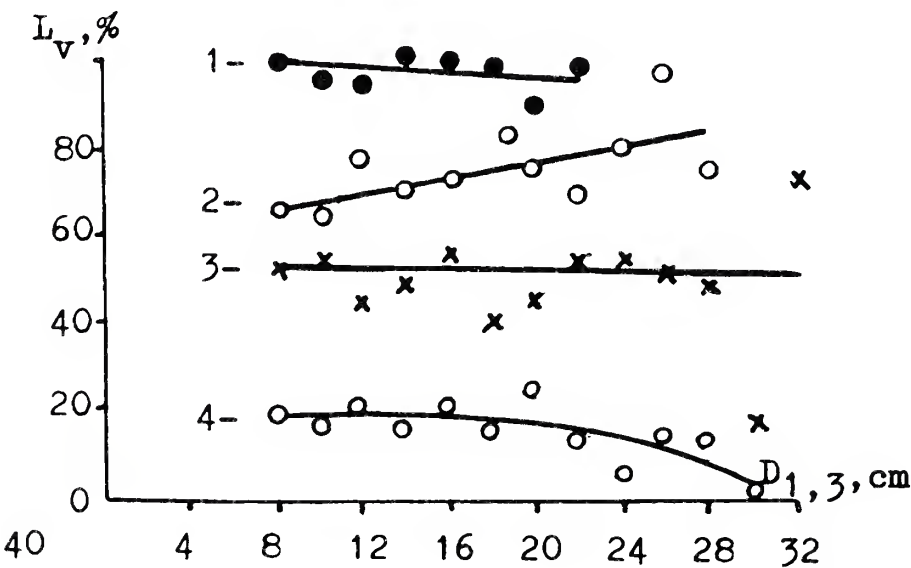


Figure 2. Effect of air pollution on sparse, uneven-aged spruce stands in the U.S.S.R.: (1) healthy (60 to 130 years old); (2) weakened (60 to 200 years old); (3) heavily weakened (60 to 200 years old); (4) destroyed (60 to 200 years old).

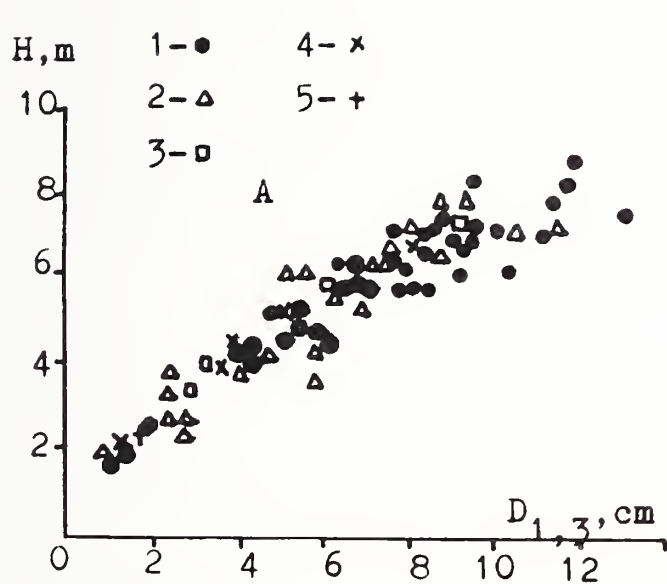


Figure 3. Effect of pollution from copper-nickel smelter on northern Scotch pine pole stand after 7 years: (1) healthy; (2) weakened; (3) heavily weakened; (4) dying; (5) dead.

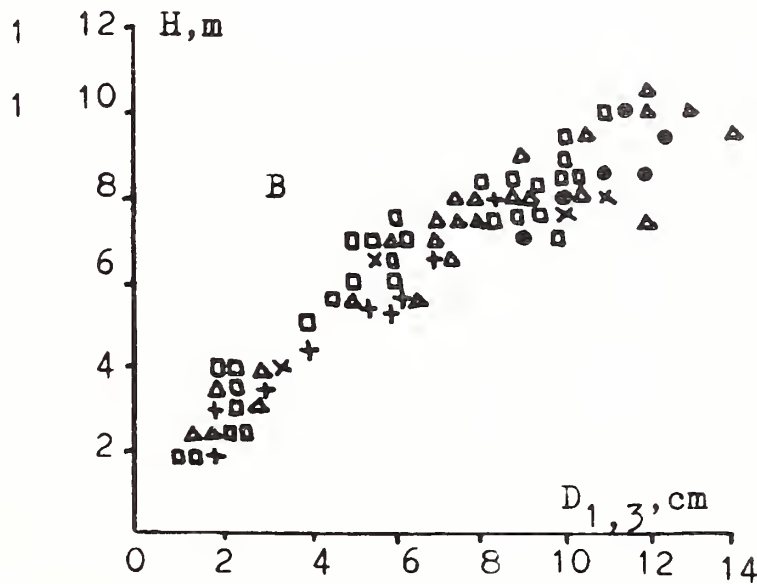


Figure 4. Effect of pollution from copper-nickel smelter on northern Scotch pine stands after 14 years. Legend- Figure 3.

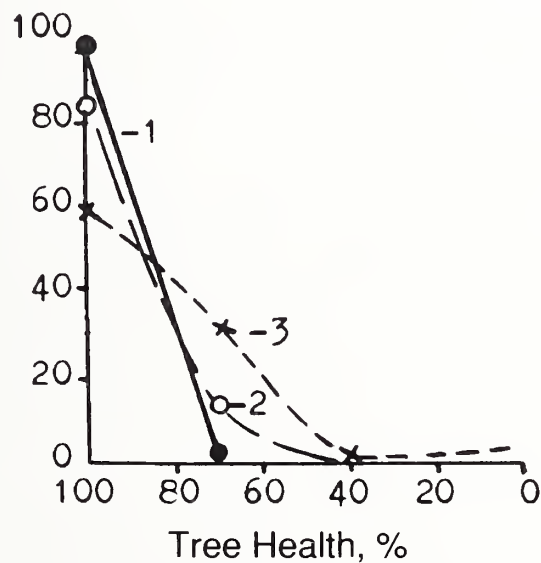


Figure 5. Age distribution of healthy northern Scotch pine stands: (1) 27 years old; (2) 45 years old; (3) 300 years old.

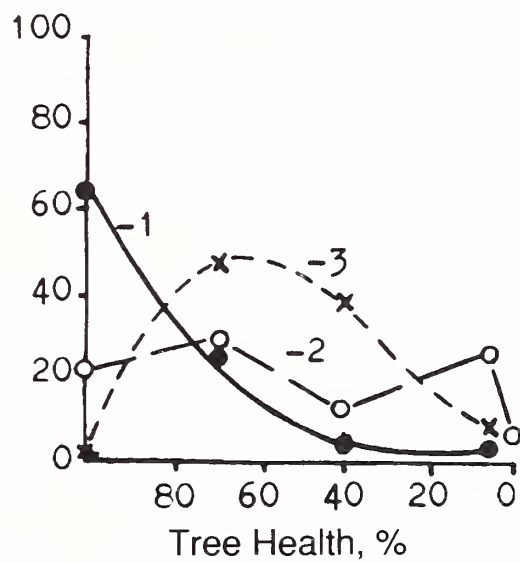


Figure 6. Age distribution of damaged northern Scotch pine stands and distance from copper-nickel smelter: (1) weakened, 34 years old, 40 km from smelter; (2) heavily weakened, 60 to 300 years old, 40 km from smelter; (3) heavily weakened, 45 years old, 15 km from smelter.

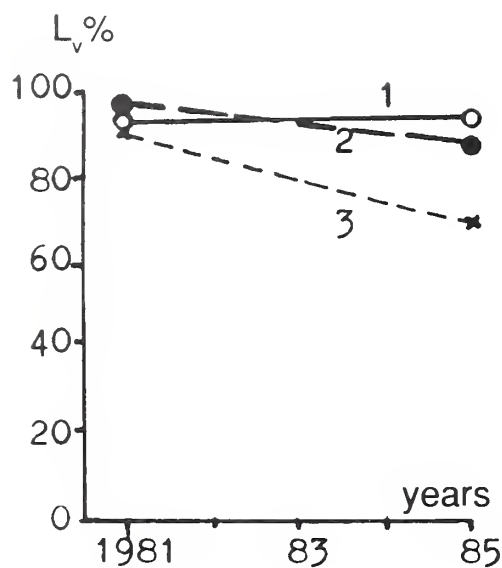


Figure 7. Effect of pollution on three-generation northern Scotch pine stand 70 km from copper-nickel smelter: (1) 60 to 90 years old; (2) 120 to 160 years old; (3) 240 to 320 years old.

The region features widespread Scotch pine (*Pinus sylvestris* L.) and spruce (*Picea obovata* Ledeb., *P. x fennica* (Rgl.) Kom.) forests. The stands generally have low productivity (growing stock 60 to 140 m³ ha⁻¹). The pine forests are even-aged or consist of two to three generations. The spruce forests are uneven-aged. Where there is no pollution, the stands are healthy or weakened. The latter condition is primarily the result of fires or advanced age (300 years or more).

One of the important peculiarities of stand structure is small canopy density (30 to 50 percent, usually attributed to poor soil conditions). In this situation, the influence of phytocoenosis on tree differentiation and vitality is minor. In overstocked or fully stocked even-aged forests of the southern taiga, there are many stunted, heavily depressed, and dying trees (Fig.1 (1), (2)). In understocked, even-aged or uneven-aged forests of the northern taiga, damage was not observed (Fig.1(3); Fig. 2 (1)) or was less severe (Fig.1 (4); Fig. 3).

The healthy trees in healthy stands always control the above-ground space of the forest: they are dominant in sparse pole stands (Fig. 5

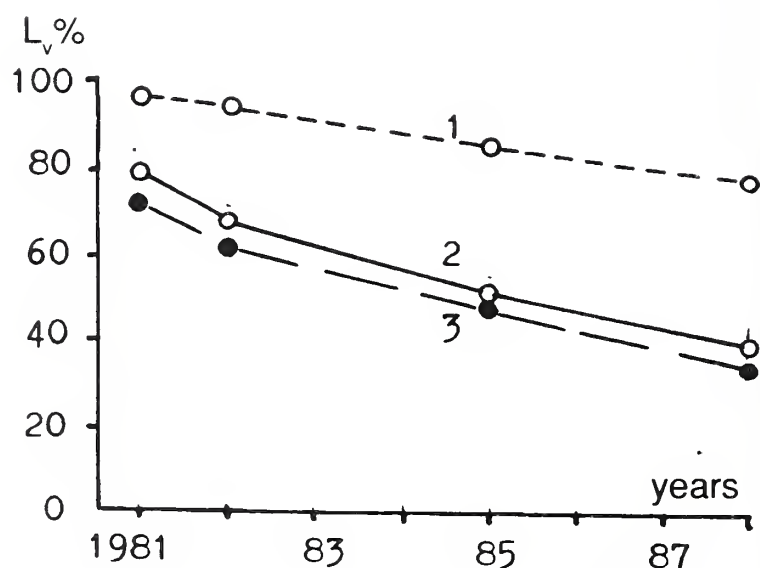


Figure 8. Effect of pollution on three-generation northern Scotch pine stand 60 km from copper-nickel smelter: (1) 60 to 90 years old; (2) 120 to 160 years old; (3) 200 to 260 years old.

(1)) and are slightly less dominant in stands of greater canopy density (Fig. 5 (2)). Their role is minor in very old forests (Fig. 5 (3)).

Air pollution substantially changes the proportion of healthy, weakened, heavily weakened, and dead trees (Fig. 6). In sparse forests, tree damage occurs independently of tree size (Fig. 2 (2), (3),(4)).

The literature contains data reporting mainly damage and death to tall, healthy trees, or to stunted and depressed trees. The data, however, show no connection between tree damage and tree size. These facts do not contradict one another, as they may seem to do at first glance. The following explanations are possible: If the slowing down of air turbulence and the lowering of the rate of deposition (absorption) of the damage-causing pollutant proceed at the varied heights of stand more rapidly than the loss of the health via phytocoenosis reasons, then the largest trees will suffer more intensively. On the other hand, if the tree differentiation caused by phytocoenosis is faster with canopy depth than the changes in damaging pollutants, then the faster growth causes damage and death to the small, weakened trees.

An inventory of damaged stands near the copper-nickel smelter allows us to draw conclusions about the more rapid damage in older stands. In 1981, pine stands that were 250 to 300 years old and 15 to 25 km downwind from the smelter were destroyed ($L_v = 5$ to 20 percent); those 30 to 45 km away from the smelter were damaged ($L_v = 40$ to 70 percent); and stands 70 km from the smelter showed no signs of pollution injury. At the same time, pine pole stands 15 to 25 km from the smelter showed moderate damage; those 30 to 45 km from the smelter suffered only slight damage ($L_v = 83$ to 90 percent); and stands beyond 45 km had no visible injury.

In recent years the spread of pollution and resulting stand destruction has continued; the initial stages of stand weakening have been observed more than 70 km from the smelter (Fig. 7). It is important to note that the weakening of trees — the appearance of chlorosis — is indicated primarily by the premature shedding of needles.

Figures 3, 4, 7, and 8 give some indication of the rate of change in the health of trees and generations of forest. The rate of health loss for some trees has reached 15 to 30 percent in individual years. For generations of trees and stands as a whole, the change in health rates at the same location has proceeded more slowly (rarely 10 percent per year). Total destruction of healthy stands may be observed in this region in the next 15 to 20 years.

Literature Cited

- Alexeyev, V.A. 1982. *Peculiarities of forest stand description under air pollution impacts. Interactions between forest ecosystems and air pollutants*. Tallinn, U.S.S.R.: Academy of Science of the U.S.S.R. 1:97-115.
- Alexeyev, V.A., and L.S. Dochinger. 1981. *Forest ecosystems and air pollution*. Moscow, U.S.S.R.: Academy of Sciences of the U.S.S.R. 5:64-71.
- Dassler, H.G. ed. 1981. *Air Pollution Impacts on Vegetation*. Moscow, 181 pp. (in Russian).
- Malhotra, S.S., and R.A. Blauel. 1980. *Diagnosis of Air Pollutant and Natural Stress Symptoms on Forest Vegetation in Western Canada*. Inf. Rep. NOR-X-228, Ottawa, Ontario. Canadian Forestry Service, Forest Research Centre. 84 pp.
- Muir, P., and P. McCune. 1987. Index construction for foliar symptoms of air pollution injury. *Plant Disease* 71(6):558-565.
- Reuther, M. 1987. Wie kvank ist unser wald? GSF: Mensch + Umself, Sept.
- Skelly, J.M., D. Davis, W. Merrill, et al. 1987. *Diagnosing Injury to Eastern Forest Trees*. University Park, PA: The Pennsylvania State University. 122 pp.
- State Committee of Forest Management of the U.S.S.R. 1970. *Sanitary Rules in Forests of the U.S.S.R.* Moscow, U.S.S.R.: State Committee of Forest Management of the U.S.S.R. 16 pp. (in Russian).
- U.S. Environmental Protection Agency. 1978. *Diagnosing vegetation injury caused by air pollution*. Washington, DC: U.S. Environmental Protection Agency, Office of Air and Waste Management. 306 pp.

Modeling Tree Level Processes

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Abstract

An overview of three main types of simulation approach (explanatory, abstraction, and estimation) is presented, along with a discussion of their capabilities, limitations, and the steps required for their validation. A process model being developed through the Forest Response Program is used as an example. In construction of this tree process model, the various organs (such as foliage) are simulated using a modular plan of development.

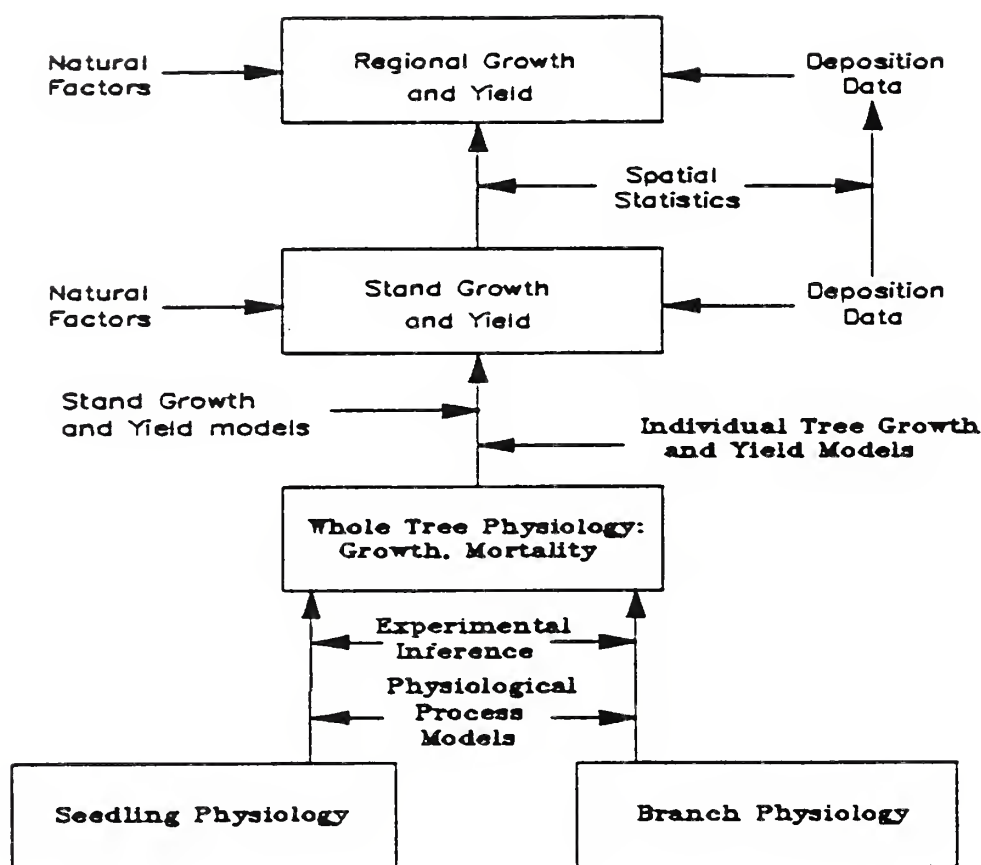
The foliar processes module is used as a reference point in the discussion, and is under development using the explanatory approach. The lower hierarchical level of processes, such as photosynthesis and nutrient allocation, is emphasized in simulation of the activities of the foliar organ. A branch growth module with which the foliar module will be coupled in the system, is also a process model, but is under development using the abstraction approach. A stand model, with which it will later be coupled, has been developed empirically, using the estimation approach. The development of modular simulators of subprocesses, utilizing various of the three developmental approaches, then coupling them is a robust approach to meeting information needs. The resultant aggregate

models provide tools with the capabilities of incorporating current scientific knowledge to provide predictions which possess the characteristics of realism, generality and precision.

Introduction

Simulation with mathematical models is an analytical tool whose use is becoming increasingly widespread. It is important that general concepts pertaining to modeling approaches and capabilities be realized and stated explicitly at the onset of any modeling activity. The objective of this paper is to place in perspective various aspects of process and empirical modeling, and how they relate to the modeling endeavors of the Forest Response Program (FRP) of the National Acid Precipitation Assessment Program.

The FRP has conducted a large research effort focused on determining the effects of acid precipitation on forest development. Research within the program has been conducted at varying levels of biological organization (Figure 1), ranging from seedling to regional scale. In order to structure this acquired information in a form which would aid understanding of the acid precipitation phenomenon, a conceptual whole-tree-physiology modeling system has been de-



FRP Levels of Organization

Figure 1. Levels of organization at which research is conducted in the Forest Response Program.

veloped. The system will act as an explanatory interface between experimental information gained from seedling and branch studies, to aid in interpreting observations made at higher levels of stand and forest.

Systems can be modeled in a way that will either provide explanation, estimation, or abstract principles. The choice of a simulation objective, along with the nature of the observational information available for model construction, together determine the character of information obtained from the completed simulator. The level of biological organization for which observational data are available, compared with the desired level of prediction, also determines whether an empirical or process-modeling approach will be required. The term "empirical" pertains to models which are developed without direct reference to the biological processes involved. "Process" models, on the other hand,

are derived by mathematical simulation of the underlying physical/chemical processes presumed responsible for the activity (activities) of interest.

The purpose of this paper is to identify some of the required steps in model development. These steps include defining performance criteria, verification techniques and validation processes. In addition, I will focus on the importance of defining the scope of a model. Since two general modeling approaches are commonly used, i.e., empirical and process modeling, I will clarify the differences between them, and outline advantages and disadvantages of each. Finally, I will present an overview of a modeling system under development to evaluate and predict tree responses to air pollution. This system is an aggregation of sub-models utilizing elements from both empirical and process modeling approaches. Combining

these techniques is one way of linking foliar processes to that of a tree, and tree growth processes to that of the stand.

Model scope

Before beginning any modeling activities, the researchers developing the model must clearly state what output is needed. Will there be predictions of size? activity? diversity? The type of information to be provided must be stated without ambiguity, prior to designing the model framework.

What entities will be of concern? In this discussion, emphasis is placed on describing trees - not leaves, forests, or stomata. What is the relationship of the model to the data supporting its development? Is the model output to be within the range of that data, and can thus be interpolated? Are there measurements of tree-level parameters, such as tree height and diameter or even whole-tree mass or total photosynthesis? Such a data bank would allow interpolation between measurements to provide tree-level output. In contrast, is the output outside the range of the database? Will it be necessary to extrapolate from what has been measured or observed, and go beyond the data to make other predictions. Answers to these questions define the scope of the model.

Model assumptions

In stating the assumptions, all factors considered to have a significant effect on the behavior of the tree (variables and processes) are listed. The assumptions reveal the essence of the simplification of the physical system, and indicate how the model will represent tree behavior. If the goal is, as stated, to model the effect of pollutants on trees, the assumption will be made that particular pollutants (defined and listed) influence tree growth and functioning, affecting in some way the processes addressed in the model. The question arises then whether the mode of air pollution action on the physiol-

ogy and growth is understood.

Another decision that must be made is the level of hierarchy. The level of hierarchy represents the level of biological organization, or complexity, to be modeled. Levels of hierarchy relevant to modeling forest processes, in decreasing order, would be forest-stand-tree-organ-cell, etc. In this example, the level of concern is the individual tree. Information may be utilized from lower levels, such as that of the organ (leaves, roots, stems, branches). One could also use information from progressively lower levels of organization - the cell level, the organelle level, or even the molecular level. Information from higher levels of organization (for example, the stand or region) will not be as directly useful in model development, but provides information characterizing constraints to system behavior. In this example, the behavior of the tree is simulated by aggregating submodels simulating behaviors of various organs and physiological systems. The functioning of these organs and systems, in some of the submodels, is represented by the behaviors of their particular subprocesses. In the foliar module, the lower hierarchical processes of ontogeny, nutrient cycling, and photosynthesis are represented.

Model building: steps, performance, verification and validation

In forestry, seedlings are often used in experiments as surrogates for mature trees. How to make the link between the entity in which we are interested (tree, in this case) and the entity observed (seedling) is an unresolved issue. How can one go from studies on seedlings of the kind so frequently undertaken, to understanding effects on whole mature trees, or from seedlings to forests? How should the extrapolations be drawn? We can design experiments, we can test hypotheses on needles, on branches, but we still have difficulties in observing and understanding the whole tree, especially a large whole tree.

Modeling is a technique particularly suited to providing links between information at varying levels of biological complexity. In this case, the challenging link is from information taken from seedlings and laboratory studies, to inferences about whole trees and forests. To properly apply these modeling tools, a clear understanding of the different types of models is first needed, along with the types of information provided thorough their use. Basic strategies for simulation apropos of the creation of a model-based approach to tree level investigations are reviewed here.

The process of modeling is often difficult to discuss. The difficulty arises not so much from its intellectual rigor, but rather from a failure to define clearly the relevant terms. Thus, one of my goals will be to focus on concise definition of

terms. Modeling requires a simplification of processes and systems of processes, facilitating analysis of their behavior. The more complex the model, the more difficult the analysis of the represented system becomes. The first concern, therefore, in model development, is to try to maintain as much simplicity as possible. The ultimate utility of the model depends on successful simplification of the problem.

A typical sequence of activities associated with scientific research is outlined in Figure 2. The prelude is the creation of the proposal, followed by research and implementation. The proposal establishing a modeling effort would be expected to include:

- 1) defining and bounding of the problem,
- 2) identification of goals and objectives,

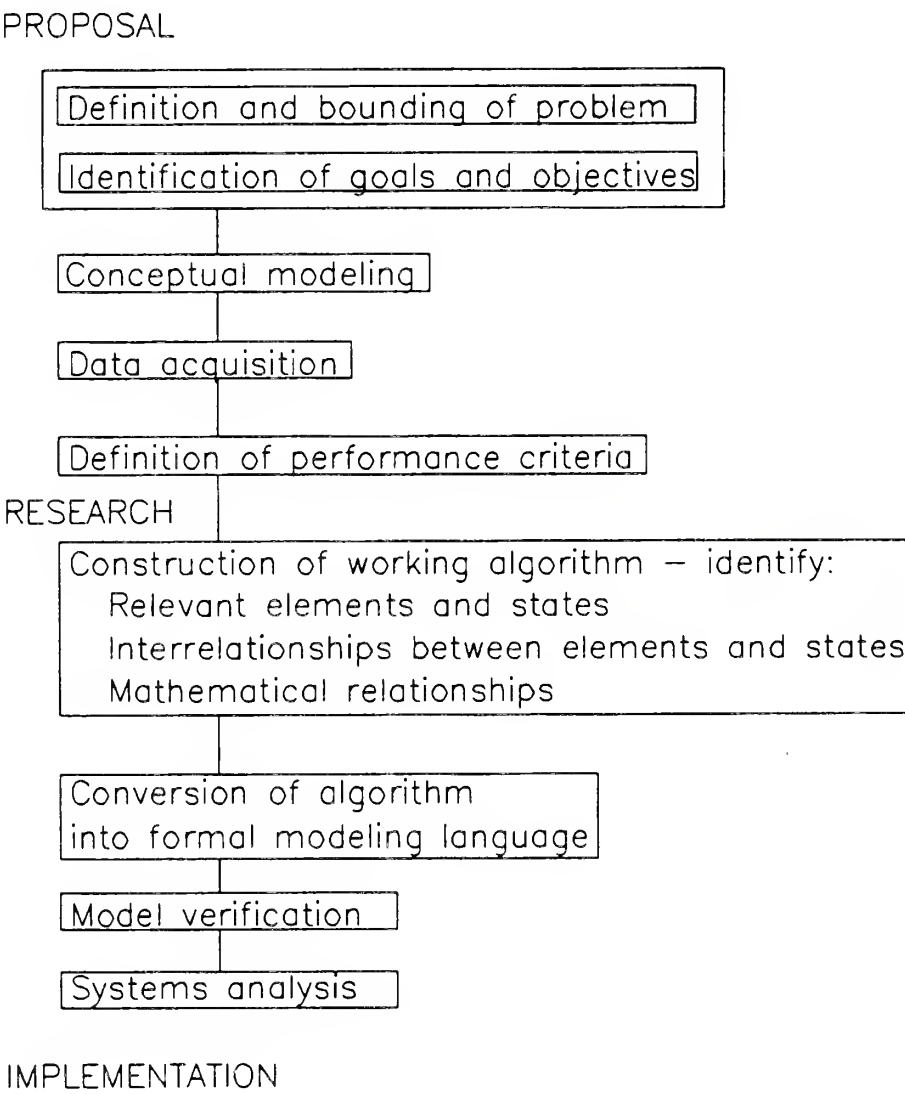


Figure 2. Procedural steps in a research program, and their sequence of execution.

- 3) citation of relevant data (whether it resides in the literature or will be gathered specifically for purposes of model development),
- 4) definition of performance criteria

I will use the Foliar submodel of the whole-tree modeling system as an example. The objective of the development of this model is to characterize the effects of acid precipitation on foliar processes of a mature conifer. Lying within the bounds of the system are the various foliar processes which are most likely to show the influence of atmospheric pollutants, and external to the system are the environmental conditions, which act as input.

Performance criteria are the standards by which the model will be judged. The specification of performance criteria provides a measurable scale against which the success of the model will be judged. Before the onset of the modeling activity, the levels of precision required of the model must be defined. Establishing precision identifies the level of complexity that must be included, and helps to define the goal. The Foliar model will be expected to reflect the trends observed in experimental research on acid precipitation, and to provide that information to the other elements of the whole tree aggregate model so that the implications of these changes in foliar behavior on whole tree growth may be explored. In this way, the Foliar model will act as an aid in interpreting those experimental results which may have appeared inconclusive.

Modeling research begins with construction of the working algorithm, which identifies the basic features of system operation. In this step, the elements of the system are defined, along with their state descriptors. The state variables, when taken together, describe the status of the system. The questions addressed are:

What element is of concern?
How does it change?

What does it change to?
Where does it start?
Where does it move to?

In the Foliar model, the element of concern is the foliage (needles) present on the various branch segments of a branch extending from the main bole of a mature conifer. Of specific interest is its changing developmental status from first emergence to death and abscission from the branch. Foliar functions which reflect this changing status include growth, aging and senescence; nutrient dynamics; and net carbon production. The states of interest therefore include nutrient status, carbohydrate status, needle age and needle amount.

Interrelationships between the elements of concern and the states of those elements are defined customarily by expression of the various mathematical relationships linking system elements. The algorithm is then converted into a formal modeling language. Forrester flow diagrams are common, followed by translation, through one of many computer languages, into executable code.

Model verification follows codification of the model. Sometimes this step is attained, yet unfortunately, it often is not. Model verification differs radically from model construction. Through verification, the simulated system behavior is compared with observations made in real life, and adjustments in the model are made where necessary. This calibration step provides the final opportunity to modify system organization before systems analysis and validation.

Systems analysis is a systematic approach for defining the character of the simulator through an analysis of the internal interactions in the model. The goal is to define the consequences of variation in values of represented system states and rates, and predict resultant repercussions throughout the rest of the system.

Verification differs significantly from validation. Validation is the exercise of proving that the model is, in fact, true. It is fairly common knowledge in the world of science that a theory can never be proven true. The theory can, rather, only be proven false or fail to be invalidated. A model is an aggregation of theories and hypotheses. As the singular theory, the model can also never be proven true, but can only hold up under the tests made against it to date.

With planning, work, and luck, the process of model development reaches the implementation stage, and the work is finally put to use.

Empirical models and process models

Two general methods are commonly used in modeling, the empirical- and the process-modeling technique. Both methods have strengths and weaknesses, and both are necessary for comprehensively addressing complex systems. Empirical modeling is an approach that is frequently used in forestry. Model

output is at the same level as that of the data. In order to model a tree, tree-level information would be required. The field of forest science has a strong history of very effective empirical modeling (Raushcer and Michael, 1987; Bruce, 1988).

In the process model, on the other hand, the outputs (or the predicted values) are at a higher level than the data. To construct a process model of trees, we would use information from the level of the organ (or perhaps an even lower level). A general rule of thumb in modeling is to avoid spanning more than three levels of hierarchy in a single model. The lower level would provide insight into system behaviors observed at the "intermediate" level. The highest level involved in the simulation reveals the impact of the simulated activities at the intermediate level. The success of an attempt to span a number of levels, such as an effort to model trees directly from the level of the organelle, for example, would be questionable.

The information embodied in functional

<u>Empirical model</u>	<u>Process (mechanistic) model</u>
<ul style="list-style-type: none">- levels of prediction and empiricism coincide- correlation between variables represented"Top-down"- many approximations & assumptions hidden	<ul style="list-style-type: none">- level of empiricism lower than level of prediction- causality between variables explicitly represented"Bottom-up"- many more approximations & assumptions explicit
-- initial information content may be no different --	
	<ul style="list-style-type: none">- greater potential for improvement

Figure 3. Contrasting characteristics of empirical and process models.

relationships of the empirical and process models also differs (Rauscher and Michael, 1987). The general form in which the ideal empirical model is expressed is:

$y = f$ (measured factors, non-measured factors, measurement error) for a given response y . The form taken by the process model is $y = f$ (measured factors, measurement error), with the assumption that all factors known to influence y significantly have been accounted for. The definition is very precise here. All factors known to influence y significantly. The determination of significance is a subjective judgment. The implication is made that the system is well understood.

Characteristics of empirical models and process models are contrasted in Figure 3. The level of empiricism is lower than the level of prediction in the process model, whereas they coincide in the empirical approach. Empiricism is common in process models, but the role it plays is different than in the empirical model. The role of the lower level empiricism in the process model is to explain why a process occurs, rather than to predict what the process does. The level of empirical information is lower than the level of prediction.

Correlation between variables is characteristic of empirical models. One event has been observed to accompany another, whether or not the phenomena have a cause/effect relationship. Indeed, it has often been stated that correlation does not imply causality. In contrast, the process model emphasizes causality. What are the cause/effect relationships? A great deal of effort is spent determining ultimate causes of the system behavior. A number of changes have been measured in plant growth when the plants are exposed to pollutants. But are those changes causes or are they effects? It may be possible that a few cause/effect relationships, coupled with normal linking of feedback and regulatory systems within the plant would predict all of the changes that are observed.

Empirical modeling often utilizes a "top-down" viewpoint. A pattern emerges that is visible in overview. The process-approach is more typically "bottom-up". Based on what is known about the processes in question, a simulator is constructed, and queried in an attempt to recreate observed behaviors. These trends are general, however, and it is possible to use either of the two perspectives in empirical or process-based approaches.

In empirical models, many of the approximations and the assumptions are hidden. They are imbedded somewhere in the error terms and in the coefficients. In a process model the attempt is made to make more of the approximations and assumptions explicit. It may be assumed that the plant is free from most stresses (such as those due to water or nutrient deficits, or stressful temperature conditions). Essentially, one assumes that the plant is in good shape apart from a factor that is out of the beneficial range.

It is interesting to note that similarly focused empirical and process models often initially provide the same information. However, a process model has greater potential for refinement and application to subsequent problems. As more is learned about the system, more detail can be included in the simulated processes. There is also a difference in what can be accomplished over time with each approach (Figure 4; Leary, 1985). Empirical models produce impressive results in a fairly short period of time, until the information content of the data set is fully exploited. A process model should provide an informational underpinning, providing the ability to go beyond the particulars of a given data set to general insights applicable more universally. The disadvantage is that initial progress appears much slower.

An empirical model usually arises from statistical analyses of observations taken at a given point place and time, and of given specific entities (in this case, trees). The tremendous

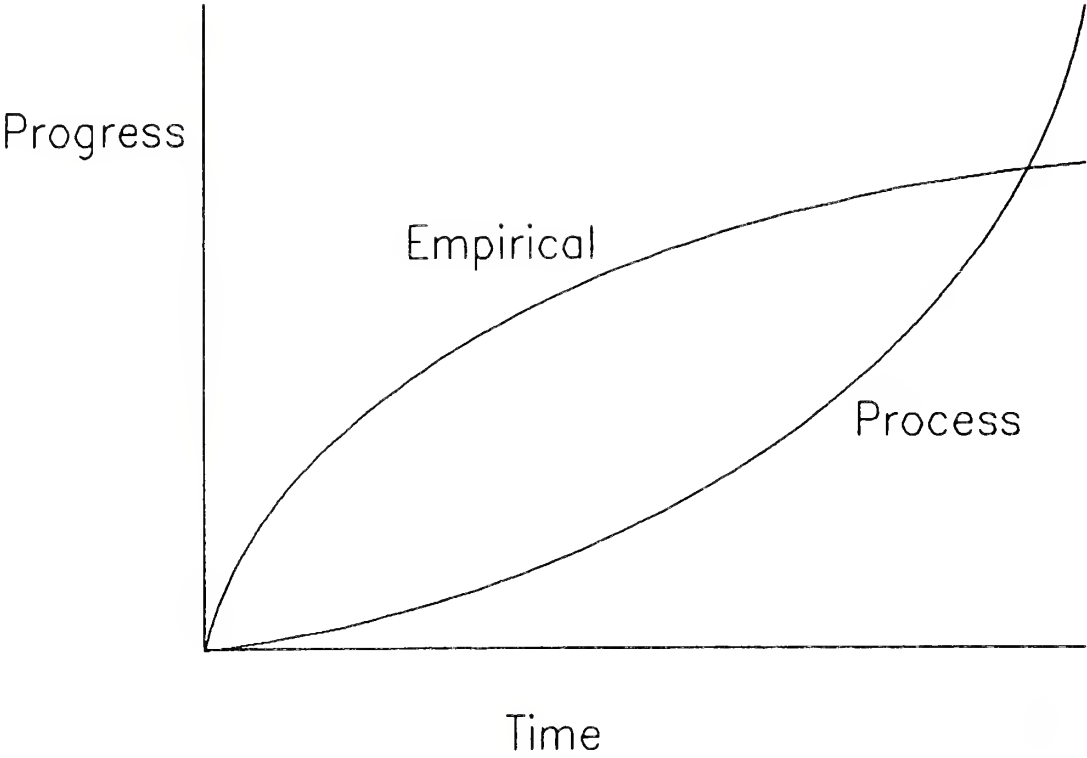


Figure 4. Perceived progress over time in process and empirical models.

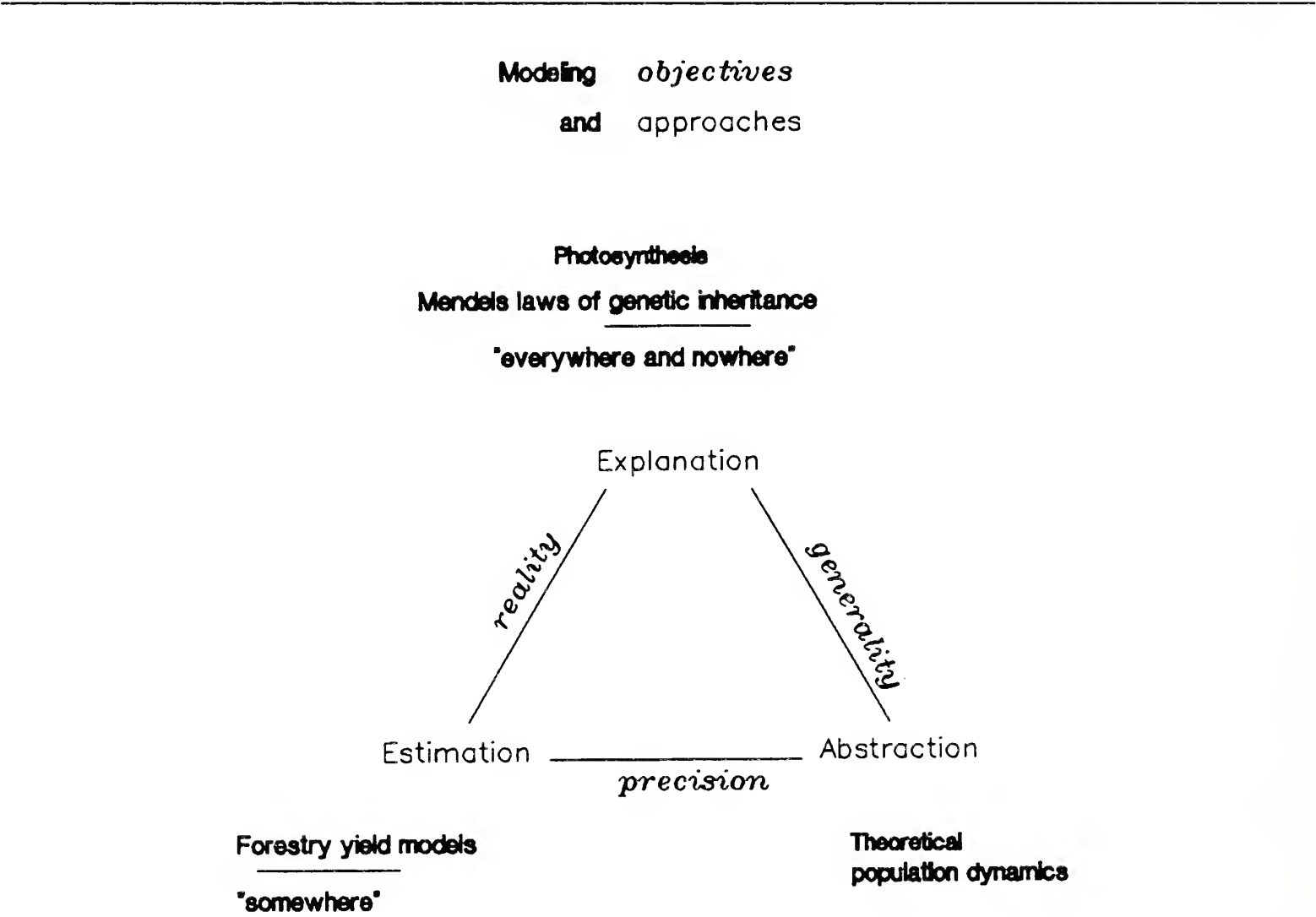


Figure 5. Objectives and approaches to modeling, with examples of each type.

variability in the genetic potential of plants to respond to various external factors has often been stated. There is variation in soil type. There is variation in climate. The empirical model can be difficult to surpass in recreating observed behavior of particular trees at a given site, for the time frame for which data was collected. What happens when events occur which those trees have not previously experienced, when the genetic stock is varied, or when extrapolations are made beyond the range of previously observed responses?

Modeling objectives and approaches

Objectives and approaches to modeling differ, as described by Levins (1966), and range can be expressed in a triangle (Sharpe, 1988) (Figure 5). Objectives range from representation of reality, to attainment of precision in prediction, to presentation of general principles. To achieve these objectives requires diversity in approach. Estimation approaches are used, for example, in the formulation of empirically-based forestry yield models. The model represents observations that were made “somewhere” (Trow, 1984), identified at a point in time, and a place. Models arising from this approach incorporate reality and precision, and commonly attain a very impressive degree of precision, but lack generality.

A second approach is that of explanation. Examples of this type of model are the traditional process models. Explanatory models apply “everywhere and nowhere” (Trow, 1984), and are represented by models such as the mechanisms of photosynthesis and Mendel’s laws of genetic inheritance. The models should apply everywhere, yet no one has observed those specific laws working infallibly in any one place. Reality is represented, with a degree of generality, but precision may suffer.

The third approach is abstraction, characterized by such methodology as that used in the study of theoretical population dynamics. The

resulting models are precise, yet describe general trends in behavior; however, they may lack the ability to depict reality.

In brief, with a single approach, one may reasonably expect to achieve any two of these three kinds of objectives but cannot expect to attain the third. It should be emphasized that the types of information available from a model depend on the modeling approach taken. A very real concern is that oftentimes information will be requested from models which were not designed to provide it, such as the use of explanatory models for the provision of quantitatively precise predictions. In such an instance, on the contrary, the other two approaches - abstraction and estimation - should be used, since they are designed to provide precise predictions.

The description of the validation process is always a challenge. Validation procedures and criteria differ for the three types of modeling approaches just mentioned, and are outlined in Figure 6. An empirical validation approach is suitable for validation of estimation models. The models are developed directly from data. Their validity can also best be judged through agreement of their predictions with independent data. The precision of their predictions can be judged via the use of statistical methods designed for quantifying precision.

The abstract and explanatory models fall into the category of process models. The abstract model is developed independently of a particular set of data, or of reality. Since the interest is not in precision of representation of a set of data, the validity of these abstract models is based instead on the correctness of the mathematical manipulations. Validation becomes more of a mathematical exercise. No particular data sets would be suitable, because all data contain various unregulated, compounding effects of genetics and environment that may differ from place to place. For example, latitude is often a very important influential

Empirical		Process	
Estimation models	Abstract models	Explanatory models	
<ul style="list-style-type: none">- developed directly from data- validity based on agreement with independent data- judged on basis of statistical precision	<ul style="list-style-type: none">- independent of data- validity based on correctness of mathematical manipulations used to develop final equation set- judged on basis of intellectual rigor consistency	<ul style="list-style-type: none">- generic concepts based on supporting evidence- validity based on their ability to interpret observed phenomena in terms of cause-effect relationships- challenging to validate- judged on basis of logic experimental evidence	

Figure 6. Validation criteria and procedures for the three types of modeling approaches.

factor in plant response. If latitude is influential, but its effects are not included, data from various latitudes would be unsuitable for validation. One conclusion is that the results of the abstract model are also abstract. The worth of the abstract model is based on intellectual rigor. The predictions are consistent and plausible, yet are not expressed quantitatively, with predictable confidence intervals. They are not designed to provide that type of information.

Explanatory models, again, are a type of process model. Data enter into explanatory models as supporting evidence, but are not employed directly in model formulation. Trends observed in the data are taken into account. The general observations that repeat time and again lend the shape to the processes being explained. The validity of these models is based on their general ability to interpret the observed phenomena, again not with precision, but with a consistent ability to predict trends. Validation is challenging, due to the question of how close is "close enough." The model may match trends, but a failure to account for all important trends may not be recognized. Observed discrepancies could arise from environmentally or genetically driven normal variation

as well as from systematic shortcomings of the model. The model structure is based on logic and experimental evidence. The model can only be validated by its ability to generally track phenomena that have been observed.

It is important to note that a model need not be restricted to a single approach. Models which have been developed utilizing different modeling approaches may be, and often are, coupled. This coupling provides the capabilities to create aggregated models capable of displaying all three attributes of reality, precision, and generality. King et al., 1988, have described a general procedure for integration of process- and empirically-based models, useful in linking physiological and forest dynamics models.

An example

The topic of this paper is the modeling of whole-tree processes. The structure of the whole tree modeling system of the FRP can be seen in Figure 7. The major processes in the system are being addressed by a number of research groups within the FRP, with the individual processes divided along either discipli-

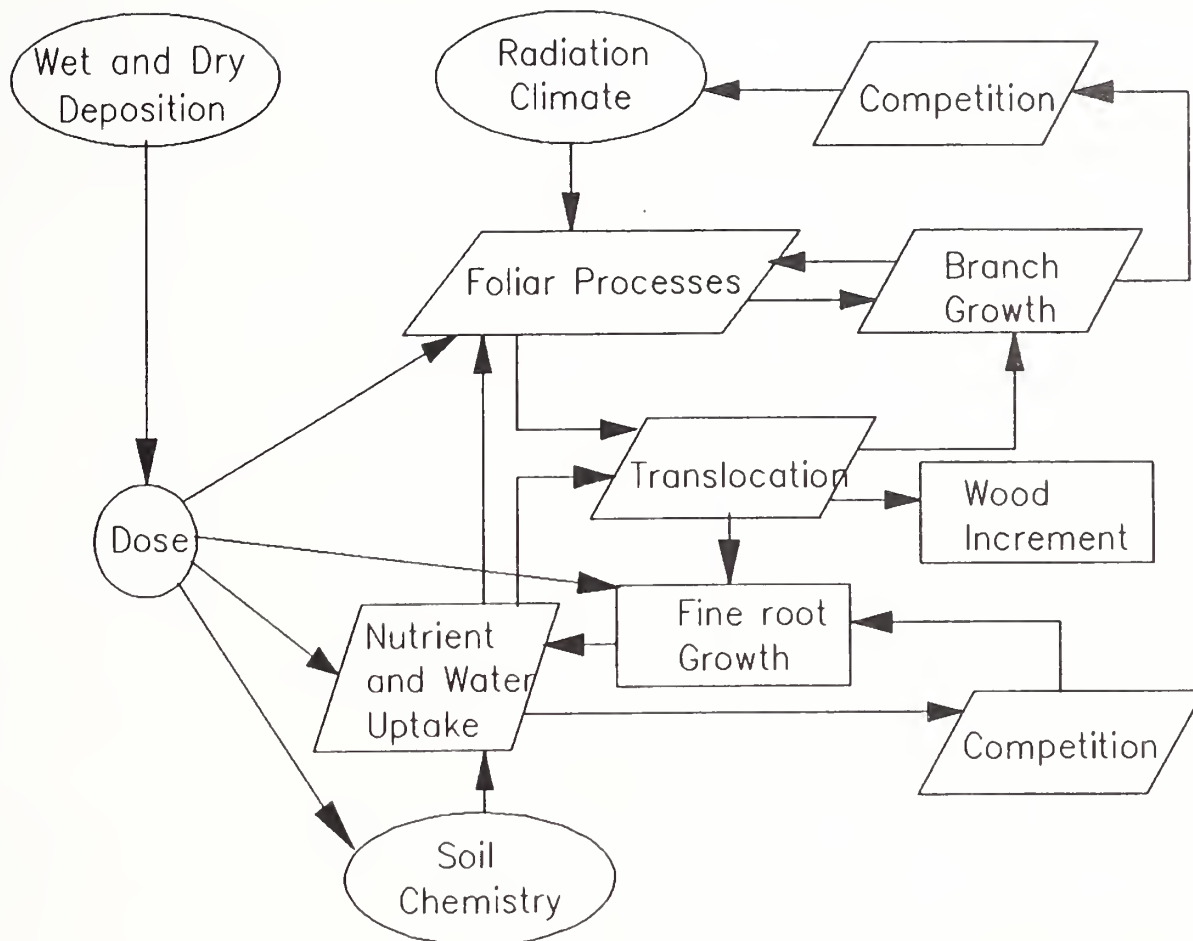


Figure 7. Schematic of a whole tree model under development to address the impact of atmospheric pollution.

nary lines or spatial orientation. To facilitate modular development efforts, the numerous processes comprising the system have been carefully delineated, minimizing required interaction between modules.

The emphasis is to simulate the effect of pollutants on the growth and changing morphology of a tree. The effect of pollutants, however, is not at the tree level, but at the levels of the numerous subprocesses acting in concert to form the tree. Research in model development is focused on determining the process, or processes, that are directly impacted by the pollutants, or defining the first cause/effect relationships which are ultimately responsible for the effect of pollutants on tree development.

One module of the system, the Foliar submodel, as mapped out in Figure 8, will now be discussed in more detail.

The major working hypothesis in the foliar processes model is that normal foliar activities are modified by deposition of the mineral elements in acid precipitation that are also used in normal needle function. Initial effects occur due to tissue damage and alteration of the efficiency of the processes such as photosynthesis and stomatal control (and ultimately respiration and transpiration). Ultimately, revision of the balances of these normally occurring foliar nutrients could reduce the efficiency of physiological processes, even without signs of visible damage.

The activities of foliage located on a given branch of a mature tree are under scrutiny. The states of interest in this subsystem include nutrient status, carbohydrate status, developmental age, and needle amount. The location on the tree, and its maturity, are conditions of the environment of the branch which also influence the values of these state variables. Foliar

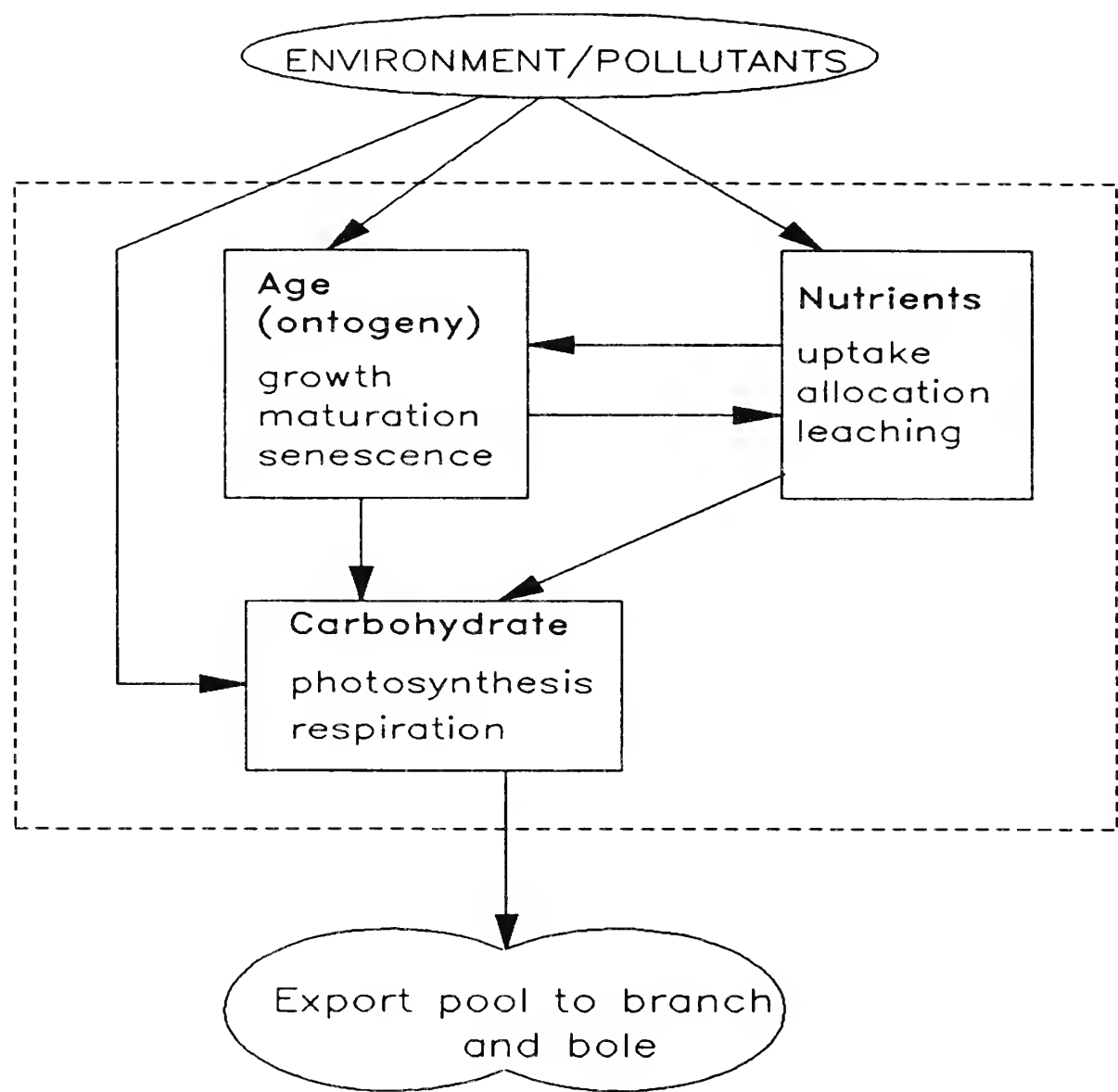


Figure 8. Diagram of processes addressed in a model of foliar processes designed to address pollution response.

functions which are of major concern in the model include growth/maturation, photosynthesis/respiration, and nutrient reallocation (Figure 8). Although foliage is not limited to these activities, the mentioned processes encompass the major avenues of acid precipitation influence on foliage. These states and processes (and their interactions) define a simplified system encompassing the dominant pollutant responses. Water use through transpiration and evapotranspiration will be assumed to be non-limiting, and is not addressed further.

Input to the system are environmental descriptors including weather and pollutant information. Supply of nutrients from the roots through the bole is input. Branch autonomy is

assumed, providing a zero carbohydrate input. The Branch model supplies morphological information on the number of branch segments of each type (age cohort and their order).

Output from the system will be net carbohydrate available for branch- and bole-wood growth and respiration. Information generated within the model are the values of the previously listed state variables. This net carbohydrate is the main contribution of the foliage to the rest of the tree, and as such, will be the input to other processes occurring on the tree.

Leaf area is calculated as a function of thermal time, and constants which characterize typical growth rates and maximal needle areas

of typical branches. Increase in leaf area occurs during the expansion period of needle growth. Leaf mass/unit area changes dynamically with season and age. Total leaf weight is calculated by multiplying the area of a particular segment of needles by its particular mass/unit area.

Tissue age plays a central role in the leaf model. "Age" represents physiological age, and is used as an indicator of tissue integrity. Age is calculated as a function of thermal time elapsed since needle emergence, and the expected life span of the needle tissue. At emergence of the needles, the tissue has an expected life span (in thermal time) characteristic of the species. Tissue age is predicted as a normalized value, and is the ratio of elapsed thermal time to the expected life span.

Needles grow in the spring as described above. Carbohydrate is fixed via photosynthesis during the summer growing season. During autumn, additional branch thickening takes place (as simulated in the branch growth model). If insufficient branch wood is incremented to support the foliage present on the branch (determined in the branch growth submodel), loss of the excess foliage is then predicted to occur late in the season.

Tissue nutrient concentration is governed by the rates of input and outflow from the needles. Input of mineral nutrients is from root uptake and reallocation from older foliar cohorts. Root uptake is not simulated within this model, but is accepted as input. A balanced, ample supply of nutrients from the roots is assumed, so the variable quantity determining source strength is the changing quantities of aging needles.

The rate of nutrient retranslocation is a function of relative sink and source strengths. The sink is the newly expanding foliage, and the sources are the soil and the adjacent older foliage. Nutrient loss from a foliage cohort is through reallocation to a younger needle co-

hort, and leaching. Nutrient movement through reallocation to the younger foliage is governed by season change.

Nutrient leaching is a function of cuticular resistance, rain amount, and the ion concentration gradient between foliage and rain.

A number of excellent photosynthesis models are already in existence. They range in degrees of complexity and aggregation. Two models of conifer gas exchange have been developed by Lohammar et al., (1980) specifically to provide a suitable biological background for the modeling of plant growth. One model is complex, and operates on a 5-minute time step, while the simplified model operates on a daily basis. The simpler version will be employed to provide photosynthetic calculations required in the Foliar processes model, providing estimates of daily net photosynthesis, transpiration rate, and water potential.

Photosynthetic capacity declines with leaf age, and in many cases reflects a reallocation of nitrogen (Chabot and Hicks, 1982). Photosynthetic capacity in the model is therefore governed by leaf age and nitrogen concentration.

Like the concentrations of mineral elements, foliar supplies of carbon also change over the growing season. A within-leaf storage pool of labile carbohydrates contains carbohydrate that is not used immediately in growth. The rate of movement of this stored carbohydrate is a function of season, which governs the movement between foliage and other tree organs (roots, branch and bole meristems).

In the Foliar model, emphasis is placed on the simulation of chronic damage by atmospheric pollutants, where foliar activities are hampered, rather than irreversibly and radically altered. Simulation of the complications of damage due to more severe disruption are beyond the scope of the model.

Changes in net carbohydrate production induced by pollution are modeled in two ways, one immediate and the other long-term. Immediately, atmospheric pollution decreases the photosynthetic efficiency of the foliage for the day of pollution exposure. Exposures to chronic levels of pollution decrease the life expectancy of the tissue. The result of this decreased life expectancy are that the leaf tissue ages more rapidly. Leaf aging, in turn, is associated with lowered photosynthetic capacities.

The effect of acid rain on cuticle function is also simulated as an acceleration of the aging process, similar to the method used for chronic air pollution effects on tissue maturity. With increased age, retention of moisture on the leaf increases, representative of increased surface roughness. As the cuticle ages, it also provides lower resistance to leaching, thus resulting in greater rain-induced nutrient loss.

Conclusions

A common basic assumption in tree simulation is that of the maintenance of a particular allometric structure. Maintenance of a particular allometry may help to constrain model predictions to those behaviors most typically observed. However, the constraining effects of fixed allometry may prove to be a serious downfall in predicting the effects of environmental changes. Environmental stresses can affect the trees in such a way as to disturb their generally-observed regular structure. This realization requires the formulation of a more mechanistic approach to the regulation of morphology. The linking of a model simulating changes in foliar status to the model of branch morphology as described above, is a step toward determining the cause-effect nature of evolution of tree form.

The Foliar processes submodel will also serve to extend a model simulating stand-level processes. In this role, foliage is addressed at the canopy level, rather than a single branch.

Because of their empirical background, stand models embody the attributes of reality and precision. Numerous empirically-derived stand models are in existence that have a history of satisfactory performance.

In the FRP's regulatory objectives, a reasonable level of precision is required. However, predictions will be made for responses of trees to air pollution which are expected to occur outside the range of the environmental conditions from which most stand models have been developed. This predictive proficiency demands the capabilities of generality, which are outside the strengths of estimation models. The addition of the process-level foliar subcomponent to the empirical stand model should extend the stand model's capabilities to include generality. This union of the two methodologies should fortify the reliability of the stand model in these unknown conditions, and provide for defensible extrapolations beyond the range of the data from which the original stand model was derived.

These various model components have been developed utilizing various of the three developmental approaches. Combining them is a robust approach to meeting information needs. The aggregate models utilize the particular strengths associated with the approaches used to assemble the parts, and provide tools with the capabilities of incorporating current scientific knowledge to provide predictions which possess the characteristics of realism, generality and precision.

Acknowledgments

I would like to thank Dr. Dominique Bachellet, Dr. William G. Warren, and Dr. William E. Winner for their valuable comments.

Literature Cited

- Bruce, D., *Development of empirical forest growth models*. Presented at the conference - Forest Growth: Process Modeling of Responses to Environmental Stress. Gulf Shores, Alabama, April 19-22, 1988.
- Chabot, B. F., and D. J. Hicks. 1982. The ecology of leaf life spans. *Ann. Rev. Ecol. Syst.* 13:229-59.
- King, A. W., W. R. Emmanuel, and R. V. O'Neill. *Linking mechanistic models of tree physiology with models of forest dynamics: problems of temporal scale*. Presented at the conference - Forest Growth: Process Modeling of Responses to Environmental Stress. Gulf Shores, Alabama, April 19-22, 1988.
- Leary, R.A. 1985. A framework for assessing and rewarding a scientist's research productivity. *Sciencetometrics* 7:29-38
- Levins, R. 1966. The strategy of model building in population biology. *American Scientist* 54:421-431.
- Rauscher, H. M. 1987. *Comparing empirical and explanatory models*. IUFRO S6.02 Working Party Newsletter #9. (September, 1987).
- Sharpe, P.J.H. *Forest process modeling: scope, limitations and opportunities*. Presented at the conference - Forest Growth: Process Modeling of Responses to Environmental Stress. Gulf Shores, Alabama, April 19-22, 1988.
- Trow, G.W.S. 1984. Annals of discourse: the Harvard Black Rock Forest. *The New Yorker* (June 11, 1984), pp. 44-99.

Session

III

Bioindication and Protected Area Monitoring

David Shriner, Local Organizer

Introduction

The theme of the third session of the Second US-USSR Symposium on Air Pollution Effects on Vegetation was "Bioindication and Protected Area Monitoring." The session was held at the Great Smokey Mountains National Park, an international biosphere reserve. This theme was chosen in recognition of the international need to establish coordinated programs of long-term ecological monitoring in order to be able to establish meaningful baseline databases against which environmental change in response to man's activities might be measured.

Papers on the first day of this session were aimed at a review of past and current approaches to biological/ecological monitoring and at future needs to monitor changes in the environment.

On the second day, a workshop format was used to focus discussion on the emerging issue of global climate change as an example of the need for long-term environmental monitoring. Discussion covered the measured climatic record, effects of elevated CO₂ and climate change on vegetation, and the methods available to extrapolate estimates of change to regional, continental and global scales.

On the third day, participants visited National Park Service and Oak Ridge National Laboratory research sites in the Great Smokey Mountains National Park where research on the effects of atmospheric deposition is being carried out in high elevation spruce-fir forest ecosystems.

David Shriner

Welcome and Charge to the Conference

Bioindicators, biomonitoring, natural area protection and global change—the environmental issues, scientific challenges and their interrelationships

David E. Reichle

Director Environmental Sciences Division
Oak Ridge National Laboratory*
Oak Ridge, Tennessee, U.S.A.

Ladies and gentlemen, workshop participants, speakers, representatives of sponsoring federal agencies and particularly our Soviet guests...it is my pleasure to welcome you to this second bilateral U.S./U.S.S.R. Symposium on Air Pollution Effects on Vegetation. A number of the U.S. scientists present here today enjoyed your hospitality at the first symposium in 1982 in Tallinn and Leningrad, and it is our pleasure to return your courtesy at this time.

I want to acknowledge the sponsorship of this symposium by the U.S. Forest Service and the U.S. Environmental Protection Agency. We extend our thanks to Superintendent Pope and his staff of the Great Smoky Mountains National Park for their local support. I want to thank Dr. David Shriner of the Environmental Sciences Division at Oak Ridge National Laboratory for organizing this symposium, and, on his behalf, express our appreciation to the organizers and speakers at the symposium today on Bioindication and Protected Area Monitoring and tomorrow's workshop on Global Climate Change. And, finally, we extend a special welcome to

Oleg Blum who spent several weeks working with us at Oak Ridge last summer.

The topics of discussion during the next two days are extremely appropriate for this symposium since they focus on international environmental issues and recognize the need to:

- protect natural resources
- identify the global nature of environmental pollution
- appreciate the importance of developing bioindicators, and to anticipate global change
- understand the importance of projected natural areas for long-term monitoring and research

This is also an extremely appropriate location for this symposium, since the Southern Appalachian Biosphere Reserve is a model of natural area protection, monitoring, and experimental research sites, as well as interinstitutional cooperation among all of the major envi-

*Operated by Martin Marietta Energy Systems, Inc., under contract DE-AC05-84OR21400 with the U.S. Department of Energy.

ronmental institutions in the region.

You are here in Gatlinburg, Tennessee, in the heart of the U.S. Eastern Deciduous Forest Biome glacial refugium and the region of greatest biotic diversity in the continental United States. Along the altitudinal, microclimate and soils gradients of this region are found representatives of the major forest plant communities between Florida and northern Canada. The unique research sites and collaborating institutions are represented by:

- The Great Smoky Mountains National Park and central core of the Biosphere Reserve
- The Coweeta Hydrologic Research Laboratory of the U.S. Forest Service
- The University of Tennessee
- The Oak Ridge Environmental Research Park of the U.S. Department of Energy
- The U.S. Forest Service—Cherokee and Pisgah National Forests

We are faced with a number of global environmental problems. As scientists, we have learned that few environmental insults have only local consequences—DDT and ocean dumping of wastes have clearly illustrated the global consequences of local environmental activities. As one perspective, there are a number of potential global environment issues which the U.S. Department of Energy has identified as possible consequences of energy technology development.

- greenhouse effect (trace gases)
- "Chernobyl" incidents
- acidic deposition
- coastal zone development
- geologic waste disposal
- biomass for energy
- North Slope development
- nuclear winter
- geothermal energy development

In addressing these pragmatic environ-

mental problems, as scientists, we find that they all have common scientific components and that our scientific data, understanding, and methodologies are yet inadequate to resolve these issues so that sound international environmental policies can be established. These scientific components involve determining mechanistic processes linking different subsystems and temporal and spatial scales of interfaces:

- identification of interfacial linkages
- quantification of critical processes
- extrapolation across temporal and spatial scales
- development of hierarchically nested global models
- validation and testing of global models

The key scientific challenges are those dealing with linkages among environmental subsystems—the interfaces between the biotic and abiotic environment—and also those dealing with the incongruities in scales of space and time over which different environmental processes operate. While we attempt to identify important global environmental processes, to understand how the environment works and to struggle with how to use experimental data (local site, short-term) to address environmental issues of broad scale and long-term duration, it becomes obvious that (1) we cannot afford to (nor do we have the time to) study every ecosystem in infinite detail in order to protect it, and (2) we must devise means to anticipate ecological damage before it occurs. This is where bioindicators and biomonitoring will play such an important role in the future for environmental protection.

While I do not want to intrude into the substance of the presentations at today's symposium on Bioindicators and tomorrow's workshop on Global Climate Change, I do want to stress how interrelated these topics are to the overall theme of this meeting:

- Protecting natural areas will require eco-

logical research to understand mechanisms of pollution effects

- We are dealing with an issue of global stewardship and global environmental processes
- Developing sensitive bioindicators is a necessary prerequisite to anticipating (and

hopefully avoiding) deleterious ecological effects of human activities.

Again, I welcome you; I hope that you find these topics stimulating; we are eager to exchange our thoughts with you.

Monitoring the Environment in the 21st Century¹

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Many years ago when I was a boy, there was a popular science fiction radio program whose hero fought villains and loved maidens in a future century. Because the story was derived from the fertile imaginations of skilled science writers who could draw on the principles of hard science and engineering, it was relatively easy for these writers to come up with rocket ships made of impervium whose crews were armed with disintegrator pistols. The plots, of course, were always variants of good-versus-evil. The hero, accompanied by his heroine and assisted by the old and brilliant scientist, fought to save earth—and usually his heroine—from a wide assortment of interplanetary villains.

When Dave Shriner suggested that I talk about this particular topic—monitoring in the 21st century—almost immediately I recalled the radio announcer speaking in a sonorous and stentorian voice—“BUCK ROGERS IN THE 25TH CENTURY.” I, however, kept transposing that phrase to “Stanley Auerbach in the 21st century.” There are, of course, several significant differences between those two futuristic scenarios, not the least of which is that I dis-

tinctly am not a hero soaring about by means of a rocket belt. But, more seriously, we are trying to perceive a future century whose beginning is only 13 years away, in contrast to one that is half a millennium ahead of us. We are also faced with the challenge that the realities of tomorrow are inextricably related to the problems of today. And while it might be fun to use our imaginations to predict or fantasize about likely possibilities 25 or 50 years from now, as scientists, we need more than imagination to predict events or activities in the future—especially activities which require the involvement of different societies, multiple governments, and other manifold social and political pressures.

There is an old, very familiar observation that the past serves as a prologue to the future. I think that this phrase is especially appropriate for issues of wide social, economic, and political involvement, such as those dealing with the environment. What we will be doing in the field of environmental monitoring, at least in the first half of the 21st century, is likely to be derived from the developments and issues in this latter part of the 20th century.

¹Research sponsored by the office of Health and Environmental Research, U.S. Department of Energy, under contract DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. Publication No. 3198, Environmental Sciences Division, ORNL.

We are now completing the second decade of major environmental activity in this century. Prior to 1970, public awareness of environmental issues was nearly nonexistent. Governments had little or no interest or authority to deal with environmental problems except where connections to matters of public health were too obvious to be ignored. It took a number of dramatic events to arouse public awareness to the point that it served as the essential impetus to political action. Environmental awareness rather quickly demonstrated that it knew no national borders. Earth Day and the Stockholm Conference on the Human Environment both catalyzed and crystallized the beginnings of a movement which was to transcend political boundaries and become an issue of considerable importance in most countries.

Environmental actions followed in the decade of the seventies, not only in the United States but in many other countries. New ministries for environmental protection were established, and laws were passed regulating the disposal of residuals and protecting environmental resources. Of course, the legitimacy of the environmental issue was questioned in the public arena based on economic, social, or other considerations. While this aspect of the struggle still goes on, and probably will continue for the rest of the century, the public and, therefore, the political bodies in more and more countries have recognized the legitimacy of the environmental issue. What tends to be in question is the extent of effort and resources to be used or degrees of control to be applied in the protection of the environment. Such broad questions of policy require sound information widely understandable to the public in order for positive political decisions to be made. It is the public which drives the system. I re-emphasize this well-known fact because without good information it is difficult for the public to reach a consensus.

In 1970, the U.S. Environmental Protection Agency (EPA), charged with protecting the

environment in all its aspects, was established in the federal government. Enabling legislation was passed for air, water and soil—all aimed at either protecting the environment or requiring cleanup of pollution. Cleanup included a massive country-wide construction program to build 12,000 new municipal sewage treatment plants—an absolutely essential step toward improvement of water quality in our streams and lakes. Perhaps the most influential law to be placed on the books at the beginning of this decade was the National Environmental Policy Act. This law introduced the concept of environmental impact assessment—a concept that was initially controversial but eventually served as the cornerstone of environmental programs in the United States and subsequently in many other countries as well (Hedeman, 1980). Analysis of baseline conditions was a part of the assessment process in most cases. Obviously, any predicted changes from baseline would require some kinds of systematic means to detect and evaluate change. This type of monitoring was somewhat new. Most monitoring programs of that time were, and even today are, for compliance purposes; that is, they serve a regulatory function, ensuring that standards governing the release of pollutants or noxious substances are adhered to.

By the end of the decade, environmental issues had become established as a significant political and social issue. Much progress had been made, including advances in environmental science; however, many problems and issues were still on national and international agendas. As Russell Train, EPA's second Administrator, pointed out, "The energy crisis, together with the mounting evidence that pollution is even more widespread and harmful than the Nation had realized, has increasingly brought home the fact that environment is not simply another problem to be solved or crisis to be surmounted" (1980). Rather, environment is the overall context or framework within which we must work with all the other social, political, and economic problems—especially energy.

We are finishing the second “decade of the environment.” It may be useful to reflect on the major problems that were identified at the beginning of the 1980s in order to provide perspective on the speed at which environmental problems are resolved, especially those that require new knowledge to support action. A President’s Commission (1980) had much to say about unresolved and developing environmental problems. Here are some examples of statements issued:

- “The earth’s air is seriously threatened. The three global atmospheric problems . . . are the increase of carbon dioxide retained by the atmosphere, the formation of acid rain, and the depletion of the ozone.”
- “Forests are disappearing at alarming rates with serious environmental consequences.”
- “Land use problems include the destruction of coastal wetlands and the loss of prime topsoil.”
- “Another aspect of the chemical pollution problem is groundwater contamination.”
- “The critical question now is how to anticipate the consequences of new environmental hazards, especially those of global scale.”

Now almost a decade later, we know with greater certainty that these problems are not only still with us but also will remain as challenges to both science and society for the remainder of the 20th century. The approaches that we use to understand and resolve these problems and issues in the next 13 years will provide the foundation for 21st-century activities. Moreover, it is increasingly recognized that research in and of itself will be insufficient to answer some of the key global environmental questions that will be facing us in the 21st century.

More than ever we recognize earth as a complex physical and biological system whose components are linked in complex and subtle fashions and operate through complicated biogeochemical processes and cycles. One of the most exciting developments of the latter half of

this decade is the recognition by increasing numbers of scientists from all countries of the need to study earth as a system. To this end, an international research effort, currently called the International Geosphere-Biosphere Program has been established. This program, in turn, is considered to be part of a broader effort known as earth system science. The goal of earth system science is to obtain a scientific understanding of the entire earth system on a global scale by describing how its component parts have evolved, how they interact, how they function, and how they may be expected to continue to evolve (NASA, 1986).

More than ever, we will need capabilities to determine changes and trends in ecosystems or in the environmental parameters that influence these systems. To understand many geosphere-biosphere phenomena and their interactions, monitoring over long periods will be necessary. For example, to detect and separate anthropogenically caused climate changes from natural ones and to understand the mechanisms involved may require a decade or more of accurate global monitoring of key atmospheric physical factors. Yet in comparison, we must recognize that when it comes to systematic monitoring for ecosystem change, we still face enormous challenges. In the absence of lack of fundamental understanding of many environmental processes at different scales of complexity and interaction, what to measure routinely and where and how to measure it are anything but simple questions.

Long-term monitoring strategies are deemed essential for determining changes or trends in ecological systems or in the parameters influencing these systems. Monitoring information can be made essential to hypothesis formulation, hypothesis testing, and ecological risk analysis. Perhaps the greatest opportunity lies in developing a strategy that yields information of an anticipatory or predictive nature rather than results that are retrospective.

As important as monitoring efforts are, historically, they have been characterized by numerous limitations and deficiencies. For example, monitoring programs in the past have lacked definition and long-term justification. They have failed to recognize temporal and spatial dimensions or scale. Data sets from uncorrelated monitoring programs may not have been compatible nor comparable; and monitoring efforts directed at documenting change in biological systems have not adequately distinguished between anthropogenically induced and natural changes. I am sure that other deficiencies could be added to this listing.

In spite of these problems, there is a growing recognition among responsible environmental scientists that monitoring is too important to be relegated to a scientific version of the back burner. Nor is this recognition limited to American scientists; the same viewpoints are being expressed by many of our colleagues in the Soviet Union. A recent US-USSR symposium dealing with environmental analysis provides a number of thoughts and ideas that bear on our future monitoring challenge (Schweitzer and Phillips, 1986).

One of the lessons we have learned as a result of the acid precipitation issue is that a long-term monitoring program designed and implemented today may not be directly applicable to environmental issues 50 years from now (Linthurst et al., 1986). In an analysis of long-term trends in lake acidification, a major difficulty in interpretation arose because of a change in analytic procedures from colorimetric to electrometric methods. In addition, earlier monitoring records were based on a nonstatistical sampling scheme that precluded making good estimates of precision later. There are many other examples of past monitoring studies with which one can find fault. But in each case, one must be careful to distinguish between the reasons for initiating the monitoring activity and the success with which it was carried out. As is true for all aspects of science, we

learn not only by carrying out the work but also from the mistakes that may be made.

New approaches to environmental monitoring that may have useful applications in the 21st century are being explored by our colleagues in the Soviet Union. As reported by Vasilenko and his associates, a new type of monitoring, namely, snowpack pollution monitoring, has been under way in the Soviet Union. It currently is part of the State Environmental Pollution Observation and Monitoring Service and includes observations at 1000 meteorological stations. This system provides data on the quantities of atmospherically deposited pollutants and their spatial distribution. With this system, distributional maps (either by region or for the whole country) are plotted for pollutant concentration in the snowpack, rates of deposition, nitrate and sulfate budgets, and regional maps for special pollutants such as heavy metals, benzopyrene, ammonia, and other compounds (Vasilenko et al., 1986).

Scientists in the USSR State Monitoring Service are developing a philosophy of a comprehensive and integrated system which will involve the systematic measurement of pollutant levels in the environment with concurrent hydrometeorological and biological observations. As Anokhin points out, this integrated approach offers the opportunity to establish an ecological service in the Soviet Union. Such a service could provide scientifically validated assessments of ecological consequences of anthropogenic impacts (Anokhin et al., 1986).

The use of long-term measurements to determine the assimilative capacity of an ecosystem is another area of interest to Soviet scientists. They have been particularly interested in ocean ecosystems. In describing studies on the assimilative capacity of the Bering Sea ecosystem, Izrael and his colleagues emphasize the importance of both understanding and quantifying ecosystem biogeochemical processes in order to be able to assess the

consequences of continued pollutant inputs. The key to the development of functional assimilative ecosystem models is a combination of integrated studies and a system of monitoring (Izrael et al., 1986).

Global-level monitoring has been conducted in the Soviet Union since the early 1970s at four background stations. Two of these stations are located within the European part, and two areas within the Asian part of the Soviet Union. Global air pollution monitoring is also conducted at seven background stations located in Russian biosphere reserves (Sokolovsky, 1986).

These Soviet activities are examples of widespread and burgeoning interests in and activities involving environmental monitoring being carried out in the majority of countries. In point of fact, there are so many different kinds of monitoring networks (local, regional, country-wide, and global) that simply obtaining a listing of all of them would require a significant investment of time and resources. It is precisely because of this multidimensional array that I believe it will be necessary in the last decade of this century to define and focus on key systems whose attributes will be related to specific tasks or areas. During the past year, there has been an intensive planning effort under way within EPA for a new program in long-term ecological research. A key component will be an environmental monitoring and assessment program. But unlike such efforts in the past, what is being proposed is an environmental monitoring effort that will be coupled with research and risk assessment.

Plans are already under way for the establishment of new and highly sophisticated earth system process monitoring that surely will be in place by the turn of the century. In the next decade, global measurements of the atmosphere and ocean surfaces will see increasing use of both passive and active microwave techniques, of color imaging for ocean chlorophyll,

and of vastly improved spectroscopy for chemical analyses. Lasers, remote sensing, space observing platforms, and new imaging capabilities offer tremendous possibilities for global scale environmental monitoring, and I predict that we will see many of these in operation by 1999.

But a major challenge in the 21st century will be to combine the sophisticated technology of detection, measurement, analysis, and data storage that will be available into working systems which will rapidly synthesize all these data. Literally billions of bits of information will be collected in hundreds of monitoring systems. These systems will monitor different media and different endpoints and will be hierarchical in that they will function at different temporal and geographic scales with cross linkages between systems for exchange of data. Moreover, they will be operated by a variety of organizations in different countries. Given the multidimensionality of this challenge, it does not seem likely that one should anticipate a single, all-unifying monitoring system to be functional at the beginning of the century. Therefore, the challenge in the next decade is to begin to address in a realistic fashion the questions of organization, methods standardization, centralization versus decentralization, and related aspects of establishing such systems.

How do we keep monitoring systems dynamic and not have them become mere collections of numbers and data that are not utilized beyond simple checking for compliance? I believe that they will have to be institutionalized in a manner that provides continuing challenges in the areas of synthesis and interpretation. By doing so, first-rate scientific staff can be attracted and maintained. Ideally, these advanced monitoring organizations should be linked with or be a component of a research unit that works on environmental problems at levels of organization that are compatible with those being surveyed or monitored. Intellectual dynamism needs to be ensured through ongoing

opportunities for periodic student participation in the work of the monitor center either through thesis studies or other part-time arrangements.

It is tempting to visualize large-scale monitoring centers in the next century that would look like the National Aeronautics and Space Administration (NASA) mission control centers or those of the air defense commands. Banks of sophisticated computer terminals linked through high-speed networks to scores of data banks would have large screens where operators could bring up local, regional, continental, or even global data that could be scaled, synthesized, superimposed, examined for temporal trends, or analyzed in any other way that one could conceive.

The technology for such centers is certainly available. Likewise, there are a number of monitoring ideas and approaches in environmental science that hold considerable promise for providing data that can be used proactively rather than relying on our current practice of retroactive evaluation. Systems ecologists have demonstrated that with knowledge of the dynamics of ecosystem processes and the use of coupled nutrient cycling models whose parameters and structure are based on field data, monitoring points for measurement of key variables can be identified. For example, it has been shown that a key forest ecosystem nutrient such as calcium can be monitored by periodic measurements of its concentration in soil water (Shugart et al., 1976). These data are fed into a proactive computerized model system and are a basis for determining trends in forest ecosystem health.

Another recent approach that shows promise is environmental specimen banking (Lewis et al., 1987). This is the systematic collection and storage of environmental specimens for future analysis and evaluation. If the bank is designed in such a way that the specimens and the ecosystems from which they are obtained are characterized to reflect system states, then

temporal or geographic trends in chemical pollutants can be identified. Retrospective or prospective shifts in pollutant distribution can be evaluated, and perhaps even the capability to distinguish man-induced changes from natural environmental dynamics will be developed.

Another exciting development which could have widespread application in the 21st century is the use of biosensors in monitoring instruments (Rechnitz, 1988). Biosensors are devices that incorporate biological components such as the chemoreceptor structures from organisms such as crustaceans, fish, or possibly even plants into an electronic sensor or probe. For example, a flower-blossom-based biosensor uses a cross-sectional slice of a single magnolia petal coupled to a gas-sensing electrode for amino acid measurements (Rechnitz, 1988). Other plant-based biosensors include a cabbage-leaf-based sensor to measure vitamin C, one based on soybean leaves to measure metribuzin, a corn kernel sensor that measures pyruvate, and a squash-based sensor that can be used to determine glutamic acid. There is a whole world of possibilities for the development of biosensors for the systematic monitoring of pollution effects on vegetation using plant-tissue-based biosensors. This whole field is still in its infancy but offers exciting challenges to science in the next decade because the environmental applications of this area have yet to be developed, much less demonstrated. This much is certain: the next decade will offer great opportunities to develop combination biological and chemical monitoring systems that will be unique and certainly intellectually stimulating if we choose to meet the challenge.

We are also going to enter the 21st century with problems that will impact the environment of the entire planet. Of these problems, two, it seems to me, will be major in terms of potential environmental consequences. What are these problems? The first is energy and the second, population growth. These two problems dwarf

all others in terms of their environmental consequences. But I believe that with knowledge, all problems can be addressed in a manner that is beneficial to both man and his support systems.

In that respect, environmental monitoring can and should be part of the knowledge development base in the 21st century. Since most of you will be active at least into the first part of the century, I would urge you to support the developing new efforts to create better environmental monitoring systems and to employ the special knowledge you are gaining about the effects on the vegetative components of our terrestrial ecosystems in the design and implementation of new and advanced ideas for monitoring systems in the remaining years of this century.

Literature Cited

- Anokhin, Y. A., N. Ladeishchikov, and M. I. Anisimov. 1986. A large-scale observation, assessment, and forecasting for heavy metal atmospheric transport, *In* G.E. Schweitzer and A.S. Phillips (eds.), *Proceedings of the Fifth US-USSR Symposium on Comprehensive Analysis of the Environment*. National Research Council, Washington, D.C. pp. 42-51.
- Hedeman, W., Jr. 1980. The National Environmental Policy Act. *EPA Journal* 6(10):29-30.
- Izrael, Y. A., A. V. Tsyban, G. V. Ivanov, M. N. Korsak, V. M. Kudryav-tsev, Yu. L. Volodkovich, and S. M. Chernyak. 1986. Comprehensive analysis of the Bering sea ecosystem. *In* G.E. Schweitzer and A.S. Phillips (eds.), *Proceedings of the Fifth US-USSR Symposium on Comprehensive Analysis of the Environment*. National Research Council, Washington, D.C. pp. 58-88.
- Lewis, R. A., J. Gillett, J. C. Van Loon, J. M. Hushon, J. L. Ludke, and A. P. Watson. 1987. *Guidelines for environmental specimen banking with special reference to the Federal Republic of Germany*. National Park Service, U.S. Department of the Interior, Washington, D.C.
- Linhurst, R.A., K. Thorton, P. Kellar, and D. Landers. 1986. Long-term monitoring of acidification trends in lakes: a regional perspective. *In* G.E. Schweitzer and A.S. Phillips (eds.), *Proceedings of the Fifth US-USSR Symposium on Comprehensive Analysis of the Environment*. National Research Council, Washington, D.C. pp. 6-16.
- National Aeronautics and Space Administration (NASA). 1988. *Earth System Science—A Closer View*. Report of the Earth System Sciences Committee NASA Advisory Council National Aeronautics and Space Administration, Washington, D.C.
- President's Commission for a National Agenda for the Eighties. 1980. Energy, natural resources, and the environment in the eighties. *In* *President's Commission for a National Agenda for the Eighties*. U. S. Government Printing Office, Washington, D.C. , p. 57.
- Rechnitz, G.A. 1988. Biosensors. *Chemical and Engineering News* 66(36):24-36.
- Shugart, H. H., Jr., D. E. Reichle, N. T. Edwards, and J. R. Kercher. 1976. A model of calcium-cycling in an East Tennessee *Liriodendron* forest: model structure, parameters and frequency response analysis. *Ecology* 57(1):99-109.
- Sokolovsky, V. G. 1986. Monitoring atmospheric pollution: norms and standards—policy and practice, pp. 142-150 *In* G. E. Schweitzer and A. S. Phillips (eds.), *Proceedings of the Fifth US-USSR Symposium on Comprehensive Analysis of the Environment*. National Research Council, Washington, D.C.
- Train, R. E. 1980. EPA's Task. *EPA Journal* 6(10): 7, 38-39.
- Vasilenko, V. N., I. M. Nazarov, and Sh. D. Fridman. 1986. Monitoring snowpack pollution. *In* G.E. Schweitzer and A.S. Phillips (eds). *Proceedings of the Fifth US-USSR Symposium on Comprehensive Analysis of the Environment*. National Research Council, Washington, D.C. pp. 7-25

Managing the Great Smoky Mountains National Park Biosphere Reserve for Biological Diversity

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Abstract

As an International Biosphere Reserve and World Heritage Site renowned for its biological diversity and cultural heritage, the Great Smoky Mountains National Park is one of the premiere biological reserves in the world. The regional setting for the park is described, as well as the natural and cultural resources. Management policy and programs dealing with natural resources and biological diversity are outlined. The park has long been a center of research, and for the last 15 years, a research station has been located in the park to foster research describing the park fauna and flora and ecosystem processes.

Regional Context

The ancient Appalachian Mountain Range in the eastern United States extends from Maine to Georgia, achieving its greatest elevation in the Southeast due to a massive uplift created by the collision of continental plates along a zone which is now represented approximately by the Carolinas in the United States and the northeastern coast of Africa. The Southern Appalachians form the boundaries of seven states. Due to the rugged topography, the mountainous region is relatively sparsely populated. A

large percentage remains in public ownership. In fact, it represents one of the largest blocks of contiguously held public lands east of the Rocky Mountains.

The Great Smoky Mountains National Park Biosphere Reserve lies at the heart of the region. Two companion biosphere reserves include Coweeta Hydrologic Laboratory (CHLBR) and Oak Ridge National Environmental Research Park (ORNERP). The 2,185-ha CHLBR is part of a long-term ecological research program of the National Science Foundation. A variety of experiments have been conducted on the six calibrated watersheds at the site since its establishment in 1934. Research emphasis has shifted from water quantity to water quality as various forest harvest and reforestation treatments have been administered. The 5,008-ha ORNERP site was designated in 1980. Experimental environmental research has been conducted at the site since the mid-1950s. Present areas of research include biogeochemical cycling, biomonitoring, ecosystem dynamics, toxicology and ecological effects, environmental engineering, environmental and soil chemistry, geology and geochemistry, hydrology, physiological ecology and biomass production.

Great Smoky Mountains National Park Biosphere Reserve (GSMNPBR)

Great Smoky Mountains National Park was established “for the benefit and enjoyment of the people.” This purpose was stated by Congress in the Act of May 22, 1926, that provided for establishment of the park. That act further defined the purpose in reference to the National Park Service Organic Act of August 25, 1916, which stated that the fundamental purpose of national parks is “to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations.”

The park is distinguished by the extraordinary diversity and abundance of its plants and animals, the beauty of its mountain terrain and waterways, the quality of its remnants of pioneer culture, and the sanctuary it affords for those resources and for its modern human users. The purpose of the park is to preserve these exceptionally diverse resources, and to provide to the public, benefit from and enjoyment of them in ways that will leave the resources — and the dynamic natural processes of which they are components — essentially unaltered. Some benefits and pleasures available to visitors through park programs are increased knowledge of the natural environment and cultural history, aesthetic gratification, and opportunities for rewarding recreational activities that will not seriously impair the resources.

Included within the states of Tennessee and North Carolina, the park is roughly an elliptical area of 209,000 ha and is of sufficient size to sustain self-perpetuating biological communities. The park ranges in elevation from 260 m above sea level to 2,025 m, including 16 peaks above 1,800 m, and contains 22 major watersheds, 33 clear mountain streams totaling 1,180 km, 123 individual brook trout waters, 10 major waterfalls, lesser falls and cascades that have never been enumerated,

and 668 km of foot trails through landscapes and habitats of uninterrupted natural beauty.

The area once included the major North American refuge for the preglacial warm temperate and temperate zone flora during the Pleistocene glaciation and thus has one of the nation's richest inventories of such plant groups as fungi, mosses, lichens, and hepatics. The park has a high floristic diversity (about 1,450 species of flowering herbaceous plants and 2,200 other plant species characteristic of the temperate broadleaf forest biome, with large numbers of species occurring in the same stands). Comparable flora diversity in this biome is found today only in restricted areas of Eastern China. The park exhibits almost as many kinds of native tree species (130 species) as in all of Europe. One of its major forest types, the Cove Forest, has 25 to 30 tree species, with 6 to 12 dominant on any one site. A one-tenth hectare plot may support 40 to 50 species of herbs through the seasons. The list of endangered plants that grow within the park includes 120 species. There are large expanses of virgin forest, perhaps totaling about 8,000 ha — the precise figure is impossible to calculate because some areas were logged so selectively and so long ago.

Over 70 historic structures, including four grain mills from the early European settlement period of the Southern Appalachians are located in the park, representing the finest collection of such structures to be found in the United States today.

This rich natural and cultural heritage of the park has resulted in global recognition of these values through UNESCO's designation of the park as a World Heritage site and International Biosphere Reserve.

GSMNPBR is the nation's most visited national park, recording a record 10.3 million visits last year. National surveys have shown that 1 of every 10 Americans has visited the park at least once. Again, this is a larger

percentage than that for any other national park. Visitor facilities include three visitor centers, one focusing on natural history and the other two on cultural history. There are 516 km of scenic roadway, 1,024 frontcountry campsites in 10 locations, 9 picnic grounds, 1,422 km of hiking and horse trails (103 km along the scenic Appalachian Trail), 82 backcountry campsites, 18 backcountry shelters, and 5 horse camps. During the summer season, over 100 weekly interpretive programs are offered (Peine and Renfro, in press).

This combination of extraordinary natural, cultural, and recreational resources in close proximity to the nation's geographic center of population results in the enormous popularity of this park.

Management Policy

Federal laws authorizing the establishment of the park include the National Park Service Organic Act of 1916, the Act of 1925 that authorized planning for the development of the national park in the Southern Appalachians, the Act of 1936 that authorized the development of Great Smoky Mountains National Park, and the Act of 1942 that further defined park protection. Other key federal laws dictating policy for management include the National Environmental Policy Act of 1969, the Wilderness Act of 1969, and the Clean Air Act of 1970 and subsequent amendments of 1977 (White, 1987).

The undeveloped portions of the park, 189,000 ha or 90 percent of the land base in the park, is currently being managed as wilderness, since Congress is currently considering wilderness designation of the park. The Wilderness Act reaffirms the highest standards of protection for the natural resources and their naturally occurring processes. Policies include no manipulative management, allowing naturally set fires to burn, extrapolated species reintroduction, and the control or elimination of exotic species. Human impacts are to be closely monitored and the development of additional

facilities for visitors are to be highly restricted in areas zoned as wilderness.

The primary management policy document for the park is the General Management Plan, which is both a manager's guide for meeting the objectives established for the park and a public statement of NPS management intentions. The plan establishes long-range strategies for resource management, visitor use, and development of an integrated park system, thereby creating a framework for all future programs, facilities, and management actions. This plan is expected to be in effect for the next 10 to 15 years, although some aspects of it may be altered from time to time in response to emerging needs or problems (General Management Plan, Great Smoky Mountains National Park, 1982).

In the park's General Management Plan is a comprehensive planning document called the Resources Management Plan, which describes specific programs to achieve the following management objectives:

Natural Resources Management

To protect and perpetuate the significant and diverse natural resources and ecosystems found at Great Smoky Mountains National Park, as free as possible from the adverse influences of human intrusion, consistent with legislative and executive mandates and Service policies.

To protect and, where possible, restore the natural processes as they would proceed if they had never been influenced by industrialized society.

To ensure that cultural resources and settings are maintained in a manner compatible with natural resources management objectives.

To ensure adequate protection for threatened and endangered species, critical habitats, and unusual or particularly vulnerable natural resources of the park, such as virgin forest,

brook trout habitat, beech gaps, and outstanding cove hardwood stands.

To minimize, to the extent possible, the adverse impact of exotic plants (e.g., mimosa, kudzu, Japanese honeysuckle, tree of heaven, etc.) and animals (e.g., wild hog, rainbow and brown trout) on the park's natural resources and processes.

To manage the park as the core unit of the Great Smoky Mountains International Biosphere Reserve in accordance with the objectives of the Man and Biosphere program.

Cultural resources management

To identify, evaluate, protect, and preserve the park's cultural resources in a manner consistent with legislative and executive requirements and the Service's historic preservation policies.

To reduce, to the degree possible, deterioration of historic structures that are determined, through objective evaluation, to merit long-term preservation for interpretive or other purposes.

To preserve historic structures associated with pioneer life, such as log residences, churches, schools, and barns.

To reduce and, as far as possible, eliminate the modern developments known to adversely affect the archaeological resources of the Oconaluftee-Deep Creek area, and not necessarily to the direct support of essential park programs (Resources Management Plan, Great Smoky Mountains National Park, 1984).

Resources Management and Research Issues

Exotic Species

As with almost all natural reserves (Machlis, 1985), exotic species control is a primary management and research concern. The objectives for exotic plant management within

natural zones of the park are very clear but somewhat less so in special use zones. The President's 1977 Executive Order No. 11987 on Exotic Organisms states that agencies shall "restrict the introduction of exotic species into the natural ecosystem on lands and waters which they own, lease, or hold for purposes of administration, and, shall encourage the States, local governments, and private citizens to prevent the introduction of exotic species into natural ecosystems of the United States."

In recent years the Service has become firmly committed to implementing integrated pest management (IPM) strategies where possible. These strategies employ a systems approach to pest control that may use preventive, mechanical, cultural, biological, chemical, sociological, and other tools to keep target pest populations below injurious levels. Such strategies maximize the use of natural controls while minimizing chemical treatments. IPM does not rule out the use of chemical pesticides, for in some cases, it may be the preferred approach. The choice of a chemical treatment, when absolutely necessary, should be that which is the most effective with the least potential for harm to human health and environment.

A total of 288 species of exotic plants occur in the park. Of those, only 12 are considered "problem" exotics requiring immediate management action and/or research. To date, only kudzu (*Pueraria lobata*) and mimosa (*Albizia julibrissin*) are being controlled. Research on control techniques are currently underway on princess tree (*Pawlonia tomentosa*) and Japanese grass (*Microstegium vimineum*), which is common in disturbed forest understory. Another troublesome exotic plant is Japanese honeysuckle (*Lonicera japonica*), which can spread at a rate of 15 feet per year. Like most of our exotics, it was introduced into the park by early European settlers who planted it near their homes. There are 86 known patches on the Tennessee side of the park.

The exotic plant species of most concern

is oriental bittersweet (*Celastrus orbiculatus*) because it has the ability to cross pollinate with the native bittersweet, thereby threatening the genetic base of the native.

European wild boar (*Sus scrofa*) were introduced into a private hunting preserve in North Carolina in 1912. The boar subsequently escaped and entered the park in the late 1940's or early 1950's. They have since intrabred with domestic hogs and have spread throughout the park, being most numerous in the western portion of the park.

Past and current research studies demonstrate that exotic hogs are causing considerable and demonstrable damage to the natural ecosystem. The greatest impacts occur in mesic areas and the unique highlands ecosystems; both contain numerous rare and endangered flora and fauna, and plant communities of special concern. Negative impacts have been documented in nutrient cycling, direct disruption of soils, and changes in community composition of vegetation by rooting and wallowing. Changes in vegetative cover and competition for mast crops with native wildlife are attributable to the presence of exotic hogs as well.

Accelerated control efforts in the last three years have resulted in the removal, by trapping or shooting, of over 2,000 animals. The very high fecundity rate of this animal requires that pressure continue on the animals so that hard-won gains in population reduction not be lost. This is a problem that has no ready solution and will require long-term vigilance (Tate, 1984).

Air Pollution

An air quality related research and monitoring program has been established in the park since 1977. Early projects included monitoring of precipitation chemistry, storm flow, stream pH, physical and chemical characterization of park streams, aircraft analysis of ozone concentrations, surveys of lead concentrations in plant tissues and soil litter, and evaluation of

visibility within the park (Eagar et al., 1984).

Monitoring equipment at the park's Look Rock Air Quality Station has recently been upgraded to be included in a newly established national visibility monitoring network which includes 20 areas. The network employs photographic systems to monitor views, transmissometers to monitor atmospheric optical extinction, and improved particle monitors to characterize atmospheric aerosols.

An ozone effects study has been initiated to complement the four sites in the park where ozone is being monitored at different elevations. A system of nine fumigation chambers has been established to accommodate three dosage levels of ozone.

Various native plants are being tested to document foliar injury. Extensive injury occurred this summer on 2 species tested in the chambers, and 10 additional species exhibited ozone-like foliar injury in the field and will be tested later.

An important research project in the high elevations is directed by scientists Steven Lindberg and Dale Johnson of Oak Ridge National Laboratory. Significant atmospheric inputs into the spruce-fir forests are being quantified, including precipitation, cloud moisture deposition, and dry deposition of aerosols and particulates. This process-oriented study tracks these inputs through vegetation and soils. Several similar study sites in the northwestern and northeastern United States have proven to be valuable points of comparison. Preliminary results indicate that pollutant loading in general is similar to that found in other parts of the country, but there is a much higher rate of the precipitating out of sulfate and nitrates in the Great Smoky Mountains. Studies of soil solutions indicate a significant loss of soil nutrients and the mobilization of aluminum.

The Spruce-Fir Research Cooperative coordinated by the U.S. Department of Agricul-

ture Forest Service utilizes the Clingmans Dome area in the park as one of three intensive study sites of the Southern Appalachian spruce-fir forest. This interdisciplinary research program involving 35 research projects is investigating various hypotheses of red spruce decline in the eastern United States. Not many results are in on this program and yet it is clear that the canopy vigor of the red spruce has declined sharply since the study began in 1986. There are 66 permanent vegetation plots in place in the park related to this project. Unfortunately, these studies came too late to document the biological diversity and ecological processes associated with healthy spruce-fir forest. An exotic European insect, the balsam woolly adelgid, has killed almost all the mature fir trees in the park in the last 30 years, and the study is further complicated by four years of drought unprecedented in recorded history and some unusual seasonal temperature fluctuations.

Long-term Ecological Research and Monitoring

A new initiative by scientists in the park has been to establish a structured long-term ecological research and monitoring program. This will provide a framework for future studies that will cumulatively provide baseline data on a wide variety of population dynamics and ecological processes. Key elements of the program include concentrating research in carefully managed research areas, thoroughly documented data management, involvement by numerous regional research institutions, and a long-term commitment to monitor key parameters which serve as indicators of ecosystem processes, biological diversity, and anthropogenic effects. A lack of significant funding for the program may be a blessing in disguise because it will inspire the cooperation among scientists in various institutions to become involved.

Regional Cooperation

In order to foster cooperation among the biosphere reserve units in the Southern Appalachian region, an interagency agreement has recently been signed to establish the Southern Appalachian Man and Biosphere Cooperative. Member institutions include the U.S. Department of the Interior (National Park Service and the U.S. Fish and Wildlife Service), U.S. Department of Agriculture (Forest Service, Southern Region, National Forest Systems, and Southeastern Forest Experiment Station), Tennessee Valley Authority, Economic Development Administration, U.S. Department of Energy, and the Appalachian Regional Commission (Southern Appalachian MAB Cooperative, 1988). This group will work to develop regional programs in environmental education, economic development that sustains quality natural resources, and long-term ecological research and monitoring. This program will include a periodic synthesis of research to assess the state of environment in the Southern Appalachians and suggest actions to improve conditions.

Conclusion

All the programs discussed are critical elements of our overall strategy to manage for the perpetuation of native biological diversity. We are learning as we go along. Each new research project contributes to the cumulative knowledge necessary to manage our resources effectively into the 21st century.

Literature Cited

- Eagar, C.E., P. White, and D. Silsbee. 1984. *Monitoring and research related to atmospheric deposition in Great Smoky Mountains National Park, North Carolina and Tennessee*. Paper presented at Nat. Acid Precipitation Program, Asheville, TN, Nov. 1984.
- General Management Plan, Great Smoky Mountains. 1982. USDI, National Park Service, Denver, CO.
- Machlis, G.E., and D.L. Tichnell. *The state of the world's parks*. Westview Press, Boulder, CO. 131 pp.

Peine, J.D., and J.R. Renfro. In press. *Visitor use patterns at Great Smoky Mountains National Park*. USDI, National Park Service, Southeast Regional Office Res./Resour. Management Series. 93 pp.

Resource Management Plan, Great Smoky Mountains National Park. 1984. USDI, National Park Service, Gatlinburg, TN.

Tate, J. *Techniques for controlling wild hogs in GRSM: proceedings of a workshop*. USDI, National Park Service, Res./Resour. Management Rep. SER-72, Southeast Regional Office, Atlanta, GA. 87 pp.

White, P.S. 1987. *Terrestrial plant ecology in Great Smoky Mountains National Park: A fifteen-year review and a program for future research*. USDI, National Park Service, Res./Resour. Management Rep. SER-84. Southeast Regional Office, Atlanta, GA. 70 pp. + app.

The Effect of Nitrate on CO₂ Exchange in the Epiphytic Lichens *Ramalina menziesii* Tayl. and *Pseudocyphellaria anthraspis* (Ach.) Magn. from Central California

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Recent work on the epiphytic lichen *Ramalina menziesii* Tayl. in Southern California showed seasonal effects of air pollution on physiology of this lichen (Boonpragob, 1987). It was transplanted from a relatively unpolluted area (Palomar Mountain, 100 miles south of Los Angeles) to an analogous but highly polluted location in the Los Angeles area (San Dimas Experiment Station on the south side of the San Gabriel Mountains) during three different time intervals covering a year. During the summer periods (but not the winter) the transplanted lichen died over a period of 6-8 weeks, as evidenced by a decline in photosynthesis to zero and a virtual complete conversion of chlorophylls to phaeophytins. These changes in physiological function were related to a matrix of 24 pollution parameters, of which leachable nitrate provided the highest correlation with decline in photosynthesis. Although many of the variables were highly correlated with the decline in physiological function, it seemed reasonable to investigate whether nitrate alone might have a detrimental effect on *R. menziesii* and other lichens from southern California.

Materials and Methods

The epiphytic lichens *Ramalina menziesii* Tayl. and *Pseudocyphellaria anthraspis* (Ach.) Magn. were collected from branches and trunks of *Quercus agrifolia* Neé in October 1987 at Hastings Natural History Reservation in central coastal California. After transport to the laboratory the lichen material was stored air-dry in a growth chamber at 150-200 $\mu\text{E m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR), in a 12 h light/dark photoperiod, and temperatures of $20 \pm 2^\circ\text{C}$ in the dark. Once a day, the lichens were sprayed with deionized water to reactivate physiological activity for 1-2 h in a way roughly analogous to heavy dewfall. All the experiments were completed within one month from the time of collection. Previous experiments with *R. menziesii* showed that photosynthetic rates did not decline significantly within this time-period (Matthes-Sears, 1985).

To study the effect of NO₃ ions on the lichens, 5 replicate samples, each consisting of approximately 0.5 - 0.8 g air-dry mass, were

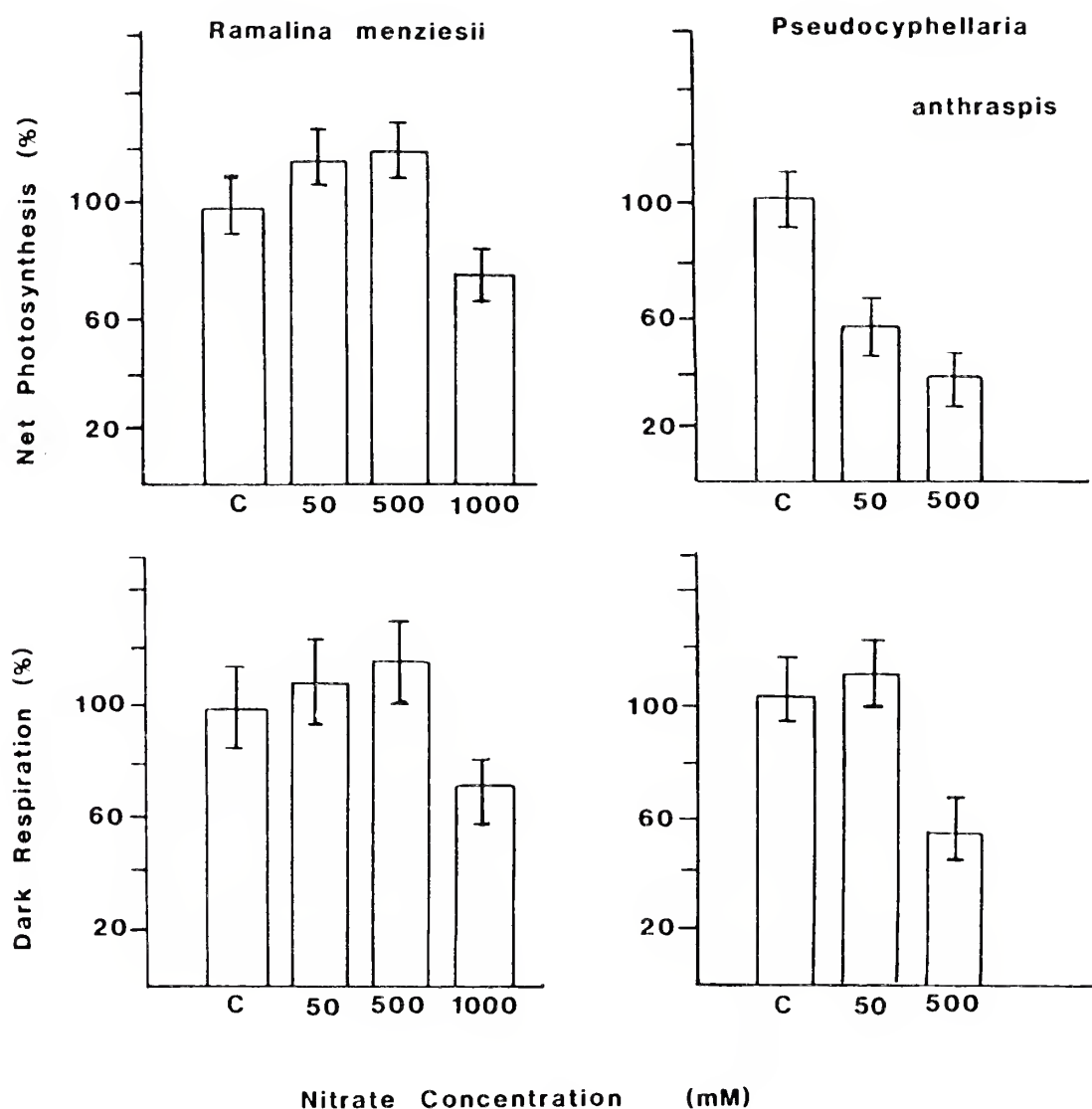


Figure 1. Effect of KNO_3 solutions on CO_2 exchange of the lichens *Ramalina menziesii* Tayl. and *Pseudocyphellaria anthraspis* (Ach.) Magn. Bars are plotted for mean ($n=5$) and 95% confidence intervals are calculated based on Tukey's HSD using the results of one-way ANOVA's (Steel and Torrie, 1960). The symbol "c" indicates the control.

submerged for 6 h in beakers with deionized water solution of KNO_3 (50 mM, 500 mM and 1000 mM) at 23°C. Control samples were submerged in deionized water under the same conditions. Before CO_2 exchange measurements were made, the lichen samples were removed from KNO_3 solutions and blotted to remove external water droplets. This resulted in a thallus water content of 120-140% of dry weight, which is approximately optimal for these species (Nash and Lange, 1988).

Net CO_2 exchange rates were measured with the discrete sampling technique (Larson and Kershaw, 1975), using an ADC 225 infrared gas analyzer (IRGA). The experimental proce-

cedure is described in detail by Matthes-Sears et al. (1987). All measurements of photosynthesis and dark respiration were made at a temperature of $20 \pm 1^\circ\text{C}$ with (PAR) at $200 \mu\text{E m}^{-2} \text{s}^{-1}$, provided by 400 W mercury multi-vapor metal halide lamp. Thallus water content was determined gravimetrically immediately after each gas exchange measurement. At the end of each experiment the samples were oven-dried at 100°C for 24 hours. All experiments were carried out with 5 replications using a program developed at the Laboratory of Mathematics at the Institute of Botany, Academy of Sciences of the Ukrainian SSR.

Results

On the basis of different CO₂ responses, *Ramalina menziesii* was more tolerant than *Pseudocyphellaria anthraxis* to the 6-h submersion in different KNO₃ solutions (Fig. 1). For *Ramalina*, no inhibition of net photosynthesis or respiration occurred after submersion in 50 or 500 mM solutions (Tukey's multiple comparison test based on a one-way ANOVA). On the contrary, a slight, nonsignificant increase (approximately 10% as compared to control) was observed. Even after submersion in 1000 mM KNO₃, net photosynthesis was 75% of the control and dark respiration was 72%.

In contrast, after submersion in 50 mM KNO₃, net photosynthesis in *P. anthraxis* significantly declined to 54% while dark respiration was unaffected. Exposure to 500 mM KNO₃ led to significant declines of net photosynthesis to 35% and dark respiration to 50%.

Discussion

Our results convincingly show differences in photosynthetic and respiratory responses in the two lichens following treatment with potassium nitrates solutions. Although *P. anthraxis* was sensitive to 6-h treatment by 50 mM of KNO₃, *R. menziesii* demonstrated an unexpectedly high tolerance under the same experimental conditions. For these species, the differences in photosynthesis and dark respiration were even more significant when the lichens were treated by 500 mM KNO₃. Even if treated by 1000 mM KNO₃ the tolerant *R. menziesii* decreased its photosynthetic and respiratory activity only by 25-30%.

A literature survey revealed little other data on nitrate impact on lichens. Barashkova (1961) in her field experiments observed stimulation by nitrates in *Cladonia rangiferina* (L.) Web. In addition, Kauppi (1980) found that increasing nitrogen with either mineral fertilizers or solutions containing NH₄⁺ or NO₃⁻ ions

produced a favorable effect on the development of *Hypogymnia physodes* (L.) Nyl. and *Cladonia stellaris* (Opiz) Pouzar & Vězda thalli. Higher contents and both greater number of phycobiont cells and a higher cell division frequency were observed. In the latter experiments, an increase in photosynthetic activity of *C. stellaris* was established by 10 mM of sodium nitrate (pH 7.7). On the other hand, the treatment with 10 mM solution of NH₄Cl (pH 6.8) led to inhibition of photosynthesis. Perhaps the inhibition was related with the effect of chloride ions in the solution (Kauppi, 1980).

Nitrates may disturb the lichen symbiosis, because stimulation of phycobiont growth leads eventually to the breakdown of symbiotic relationships and even to the death of lichens. In support of this hypothesis it is noted that the favorable effect of sodium nitrate in Kauppi's experiments was observed only during 1-2 weeks and thereafter it decreased rapidly. It is not clear, however, whether the decrease in photosynthesis was caused by the impact of nitrate ions or by unfavorable laboratory conditions during the experiment.

In general, the results obtained by Kauppi are in agreement with the experiments of Marti (1985) who studied the long-time effects of the nitrates on seven isolated lichen mycobionts. The dry mass of cultivated phycobionts increased when exposed for 20 days to 8 mM solution of NaNO₃ (pH 4.0). Particularly large increases in dry mass occurred in the phycobionts of nitrophilous lichens *Anaptychia ciliaris* (L.) Korb and *Ramalina fraxinea* (L.) Ach. According to Marti's experiments, the short-time effect of 8 mM sodium nitrate solution produced no tangible influence on ¹⁴CO₂ assimilation by lichen phycobiont. Similar results were found by Barashkova (1961) when *Cladonia rangiferina* was exposed to the effect of nitrates for a short time.

On the basis of an intensive study of an isolated phycobiont culture, Marti (1985) also

came to similar conclusions for nitrites. He found severe injury (decreased $^{14}\text{CO}_2$ assimilation by more than 50%) to the phycobiont of *Parmelia caperata* (L.) Ach. after short-term treatment with 0.1 mM NaNO_2 . Furthermore, the phycobionts of most of the 29 foliose and fruticose lichens studied demonstrated a remarkable decrease in $^{14}\text{CO}_2$ assimilation when exposed for 2 hours to 0.5 mM sodium nitrite (pH 4.0). However, relatively little sensitivity to the effect of 1 mM NaNO_2 was demonstrated by the phycobiont of *Parmelia sulcata* Tayl.; only concentrations as high as 10 mM NaNO_2 resulted in a decrease of $^{14}\text{CO}_2$ assimilation by more than 70%. Considerable differences in the sensitivity to the NaNO_2 in 2 hour experiments with isolated mycobionts were also described by Marti (1985).

Thus, literature data and our results provide evidence for the conclusion that nitrates as well as nitrites may induce injury to lichens by decreasing photosynthesis and respiration at high concentrations even after short-term incubations. It is well known in plant leaves that nitrates with sulfite reduce the levels of reductants and consequently reduce the synthesis of adenosine triphosphate (Treshow, 1984). However, the toxicity of nitrates is much less than of sulfate and sulfites (Marti, 1985; Hill, 1971; Ferry and Baddeley, 1976).

Although Boonpragob (1987) established a high correlation between absorption of NO_3 ions and photosynthetic decrease and chlorophyll degradation in the case of transplanted *R. menziesii*, it is now evident that these observations were not a direct effect of nitrates. Some experiments demonstrate a stimulating effect of low nitrate concentration on growth of other lichen species (Barashokova, 1961; Kauppi, 1980). We do not know if, in Boonpragob's experiments, the nitrate was accumulated as nitrate *per se* or whether nitrogen oxide gases were absorbed and chemically converted to nitrate. Although, Nash (1976), found little effect of nitrogen dioxide on lichens, field stud-

ies have correlated disappearance of lichens when concentration of nitrogen oxides in the atmosphere increased (Stringer and Stringer, 1974; Jurging, 1975; Sigal and Nash, 1983).

The injury observed by Boonpragob (1987) may be due to other factors. Oxidant injury to vascular plants is well known in Southern California, but short-term experiments with ozone (Ross and Nash, 1983) demonstrated no effect on *R. menziesii* even at the highest concentration ever measured in Los Angeles. Nevertheless, injury from other oxidants, such as PAN or a combination of oxidant gases, may yet prove important. Moreover, toxic accumulation of other ions is very likely. Boonpragob et al. (1988) and Boonpragob (1987) reported accumulation of 23 other ions. In the case of fluoride in particular, it is known that accumulation was sufficiently high to cause injury in a number of lichens (Nash, 1971; Gilbert, 1971).

Literature Cited

- Baraskova, E.A. 1961. Some peculiarities of growth of the fodder lichen *Cladonia rangiferina* (L.) Web. under the conditions of the Murmansk region. *Bot. Zhurn.* 46:410-413. (In Russian)
- Boonpragob, K. 1987. *Seasonal effects of air pollution on physiology of the lichen Ramalina menziesii*. Ph.D. Dissertation, Arizona State University.
- Boonpragob, K., T.H. Nash III, and C.A. Fox. 1988. Seasonal deposition patterns of acidic ions and ammonium to the lichen *Ramalina menziesii* Tayl. in Southern California. *Environ. Expt. Bot.*, 28 (in press).
- Ferry, B.W., and M. S. Baddeley. 1976. Sulphur dioxide uptake in lichens. pp. 407-418. In D.H. Brown, D.L. Hawksworth, and R.H. Bailey (eds.). *Lichenology: Progress and Problems*. Academic Press, London.
- Gilbert, O.L. 1971. The effect of airborne fluorides on lichens. *Lichenologist* 5:26-32.
- Hill, D.J. 1971. Experimental study of the effect of sulfite on lichens with reference to atmosphere pollution. *New Phytol.* 70:831-836.

- Hill, D.J. 1974. Some effects of sulphite on photosynthesis in lichens. *New Phytol.* 73:1193-1205.
- Jurging, P. 1975. Epiphytische Flechten als Bioindikatoren der Luftverunreinigungen. *Bibl. Lichenol.* 4:1-164.
- Kauppi, M. 1980. *The influence of nitrogen-rich pollution components on lichens.* Acta Univ. Oul., Sci. Rer. Natur., N 101, Biol., N 9, 22 p.
- Larson, D.W., and K.A. Kershaw. 1975. Measurements of CO₂ exchange in lichens: a new method. *Canad. J. Bot.* 53:1535-1541.
- Marti, J. 1985. Die Toxizität von Zink, Schwefel- und Stickstoffverbindungen auf Flechten-Symbionten. *Bibl. Lichenol.* 21:1-29.
- Matthew-Sears, U. 1985. *The ecology of the lichen, Ramalina menziesii.* Ph.D. Dissertation, Arizona State University.
- Matthew-Sears, U., T.H. Nash III, and D.W. Larson. 1987. The ecology of *Ramalina menziesii* VI. Laboratory responses of net CO₂ exchange to moisture, temperature, and light. *Canad. J. Bot.* 65 N 1:182-191.
- Nash, T.H. III. 1971. Lichen sensitivity to hydrogen fluoride. *Bull. Torrey Bot. Club* 98:103-106.
- Nash, T.H. III. 1976. Sensitivity of lichens to nitrogen dioxide fumigation. *Bryologist* 79:103-106.
- Nash, T.H. III, and O.L. Lange. 1988. Responses of lichens to salinity: concentration and time-course relationships and variability among Californian species. *New Phytol.* 109:361-367.
- Ross, L.J., and T.H. Nash III. 1983. Effect of ozone on gross photosynthesis of lichens. *Environ. Expt. Bot.* 23:71-77.
- Sigal, L., and T.H. Nash III. 1983. Lichen communities on conifers in southern California mountains: an ecological survey relative to oxidant air pollution. *Ecology* 64:1343-1354.
- Steel, R.G.D., and J.H. Torrie. 1960. *Principles and Procedures of Statistics.* McGraw-Hill, New York, Toronto, and London.
- Stringer, P.W., and M.H.L. Stringer. 1974. Air pollution and the distribution of epiphytic lichens and bryophytes in Winnipeg, Manitoba. *Bryologist* 77:405-424.
- Treshow, M. (Ed.). 1984. *Air Pollution and Plant Life.* John Wiley and Sons Ltd., New York, London, Sydney, and Toronto.

Environmental Monitoring of Biological Markers in Animals and Plants*

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Introduction

A plethora of environmental problems, from loss of trees in forests to massive mortality in marine mammal populations and declining fish and shellfish harvests, demonstrates the need for an integrated program of environmental monitoring. Such a program will have many elements, but one important, integrative component that will indicate the extent and the biological significance of environmental pollutants is the measurement of biological markers in animal and plant species. Biological markers, or "biomarkers," have been defined as "measurements of body fluids, cells, or tissues that indicate in biochemical or cellular terms the presence and magnitude of toxicants or of host response" (National Research Council, 1986). As such, biomarkers are sensitive indicators that toxicants have entered the organism, dis-

tributed within the tissues, and elicited a toxicological effect at critical targets (Fig. 1). Examples of specific biomarkers that are being used in this context are discussed in the section entitled Selection of Suite of Biomarkers.

In an environmental monitoring plan, a suite of biomarkers would be measured in wild animal or plant species sampled from areas of suspected contamination and from pristine reference environments. Based on the magnitude and pattern of the biomarker responses, the environmental species offer the potential of serving as:

1. Sentinels demonstrating the presence of bioavailable contaminants;
2. Surrogates indicating potential human exposure and effects; and
3. Predictors of long-term ecological effects.

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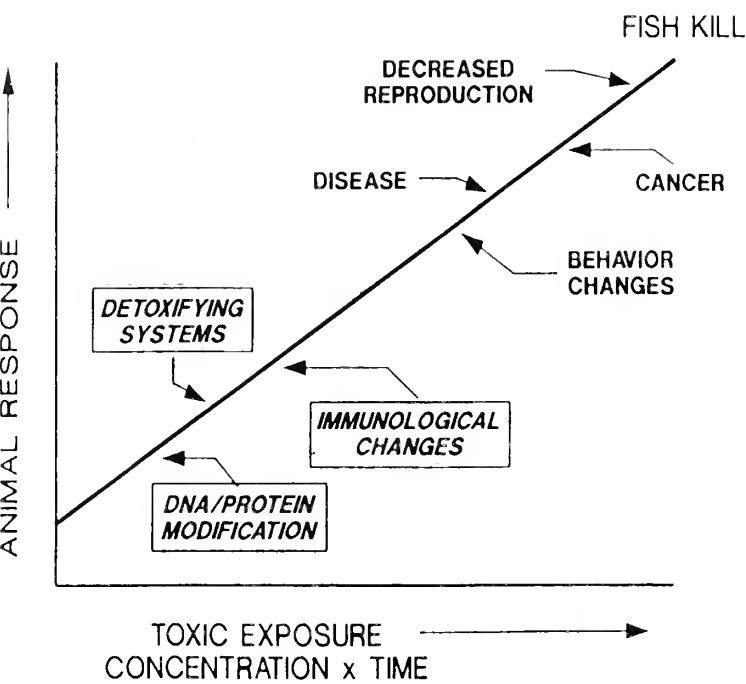


Figure 1. The Biomarker concept. The response of an animal to toxicant exposure is a function of the concentration of a chemical in the environment and the length of time the animal is exposed. We would like to avoid the long-term, irreversible adverse effects indicated in the upper right hand portion of the figure. The biomarker approach seeks to measure early responses indicated in the boxes at the lower left of the figure. These sensitive biological markers indicate that the animal has been exposed to chemicals in the environment and provide an early warning of future effects.

Justification for the Biomarker Approach

Monitoring of Environmental Species

Why monitor wild animals and plants? Data from the biological system that is the target of toxicant action provide important information that is not readily available from chemical analyses of air, water, or soil.

Temporally and Spatially Integrated Measure of Bioavailable Pollutants

Chemical analyses are expensive and provide data that are not only difficult to relate to a biological effect but may not even accurately reflect the real status of chemical concentrations over time and space. Thus, chemical sampling is like a snapshot. Changes can result from storm events, changes in winds, or intermittent releases from industrial plants. Furthermore,

contamination is often geographically patchy; a quiet pool in a stream may accumulate highly contaminated silt, while the gravel bottom a few feet away may have only trace levels of contaminants.

Pollutants associated with different environmental media have different levels of availability for uptake by organisms. Sentinel responses integrate the relative concentration and the bioavailability of contaminants, thus providing a measure that is more relevant to evaluating ecological or health risks.

Effects of realistic, low-level exposures to environmental pollutants

Extrapolation of dose-response curves to the low levels of chronic exposure characteristic of a realistic pollution scenario is one of the greatest challenges in assessing the dangers to the ecosystem or to human health. Laboratory studies are difficult and expensive, and they lack realism in the complexity of routes and types of exposure. Contaminated environments can function as natural laboratories for exploring the consequences of chronic exposure. Monitoring the biochemical and toxicological responses of naturally exposed animals helps to provide the type of information needed to analyze and interpret the results of nature's experiment.

Significance of different routes of exposure as indicated by habitat

Comparison of responses of species with different habitats, or at different trophic levels provides information on the significance of different routes of exposure. Comparisons of benthic vs. pelagic fish, foliage- vs. soil-associated insectivores, and herbivores vs. top carnivores provide contrasts in the extent of their exposure to bioavailable contaminants in water, soil, or food chain pathways. Information about exposure that occurs primarily through the food chain, for example, or through contact with sediment can help in prioritizing additional

monitoring and may suggest strategies for intervention or remediation.

Advantages of Biomarker Measurements

Measurement of biomarker responses to exposure provides information that cannot be obtained from measurements of chemical concentrations in environmental media or in body burdens. It should be recognized, however, that limitations in our current understanding of the molecular and biochemical mechanisms of toxic action often prevent unequivocal interpretation of biomarker responses, especially in relating them to a specific consequence, such as eventual development of cancer or increased susceptibility to disease.

Exposure to rapidly metabolized contaminants

Biomarkers provide evidence of exposure to compounds that do not bioaccumulate or are rapidly metabolized and eliminated, such as polynuclear aromatic hydrocarbons.

Integrate pharmacodynamic and toxicological interactions

Biomarkers integrate the toxicological and pharmacokinetic interactions resulting from exposure to complex mixtures of contaminants, and they present a biologically relevant measure of toxicant interactions in target tissues. Direct and indirect interactions of multiple contaminants upon the uptake and internal distribution of chemicals, as well as synergism or antagonism of the toxicants' action, are integrated within the organism. The biomarkers express the cumulative effect of toxicant interactions in molecular or cellular targets.

Early responses causally related to long-term effects

Many biomarkers are measures of early responses of organisms to toxicant exposure and are causally related to the expression of later irreversible consequences of that exposure. For example, genetic damage, measured

in early stages by several types of biomarkers, is understood to be initiating events causally related to the eventual expression of cancer. Likewise, early signals of impaired immune system function presage an eventual increased susceptibility to disease or parasitic infestation. Biomarkers may therefore serve as short-term predictors of long-term adverse effects.

Measures of the biological significance of exposure

Many biomarkers provide a quantitative measure of the physiological significance of toxicant exposure. For example, depression of acetylcholinesterase levels is a biomarker of exposure, but it also indicates the magnitude of the neurotoxic effect of the exposure. Biomarker responses are, therefore, relevant to understanding the relationship between exposure to environmental levels of contaminants and the potential for adverse effects at an individual or population level.

Elements of a Biomarker-based Monitoring Program

General approach

A consistent, comparable, long-term data base is needed for describing the response of a suite of biomarkers in selected environmental species from a range of geographic locations. Monitoring needs to include not only sites of known or suspected contamination but also ecologically comparable reference sites with no known sources of pollutant input. The biomarker responses of species at the pristine sites will provide a reference level for comparing responses of species from suspect sites. Statistically significant differences between sites (qualitative differences in patterns of response for a suite of biomarkers, as well as quantitative differences in the magnitude of responses) can demonstrate differences in the extent or type of pollutant exposure (Shugart et al., 1987; Loar, 1988). Differences in biomarker response over time at the same site may provide information

on environmental trends and could prove to be a sensitive and rapidly responding tool for assessing whether intervention is required or remediation has been successful. Because many of the biomarkers are short-term indicators of long-term adverse effects, these data permit intervention before irreversible adverse effects become inevitable.

Selection of Sentinel Species

Several criteria should be considered in selecting the specific species to be collected and analyzed as environmental sentinels.

Routes of Exposure

The habitat and food preferences of animal sentinels is an important factor that may aid in identifying the sources and routes of exposure. For example, where fish and other aquatic species are exposed through surface waters and sediment, comparison of water-column vs. sediment-associated species can distinguish

the contribution of sediment to exposure.

Spatial Range

The size of the home range of an animal sentinel needs to be matched to the size of the study site and the degree of geographic resolution required for a particular study. For example, voles, whose range is limited to about 400 m², were useful for studying a small site such as Love Canal. Larger sites might require the use of rabbits or groundhogs, which range over acres, and therefore integrate exposure over a wider geographic area. Although sessile animals, such as clams or mussels, provide excellent spatial resolution, there are advantages to choosing an animal that is somewhat motile because doing so can avoid anomalous results from very isolated "hot spots" of contamination.

Selection of a Suite of Biomarkers

Selection of the specific biomarkers may depend on the biochemistry and physiology of

Table 1. Benzo(a)pyrene adduct formation in DNA isolated from brain tissue of beluga whales^a. The whale population from the St. Lawrence River in Canada is declining and there have been several beached whales with bladder tumors. The area from which the whales were collected is known to have measurable levels of PCBs and PAHs, including benzo(a)pyrene. The data below quantify "adducts" [the amount of a carcinogen, such as benzo(a)pyrene (BaP), chemically attached to DNA]. DNA from the affected population of beluga whales from the St. Lawrence River has been modified by BaP at levels as high as those observed in mice and fish experimentally exposed to a carcinogenic dose of the chemical; belugas from a pristine area in Canada's Northwest Territories had no detectable adducts (Martineau, et al., 1988).

Sample	BaP adduct formation		
	Tissue	binding ^b	level ^c
St. Lawrence Estuary			
#1	Brain	206	2.15
#2	Brain	94	0.98
#3	Brain	69	0.73
Mackenzie Estuary			
#1-4	Brain	None detected	
#1-4	Liver	None detected	

^a DNA isolation and quantitation was according to Shugart et al.,1983.
^b BaPDE-DNA adducts expressed as nanograms of tetrol I-1 (resulting from binding to DNA of the anti-BaPDE metabolite of benzo(a)pyrene) per gram of DNA (Shugart, et al., 1983).
^c Level expressed as number of BaPDE-DNA adducts per 10⁷ DNA nucleotides.

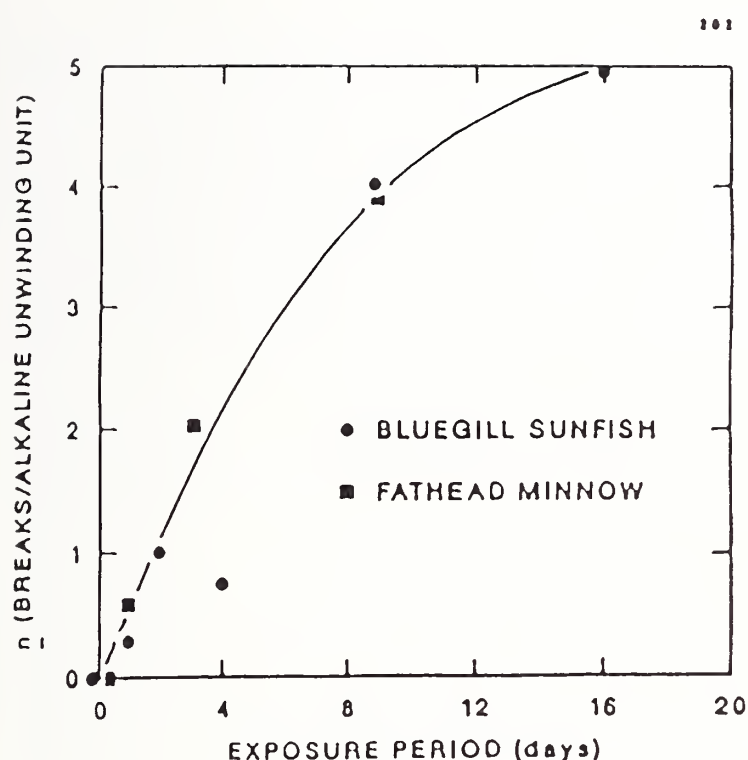


Figure 2. Time course of genetic damage, measured as the number of single-strand breaks in DNA through the use of an alkaline unwinding assay, in fish exposed to the carcinogen benzo(a)pyrene (BaP) in the laboratory. Bluegill sunfish and fathead minnows were exposed under flow-through conditions to an aqueous solution of BaP (1 ug/L) for 20 d. Results are plotted as the number of breaks per alkaline unwinding unit (see Shugart, 1988).

the environmental sentinel. Plants, for example, are fundamentally different from animals in significant ways. However, it is possible to list several classes of biomarkers that have been used for environmental monitoring and that offer promise as sensitive measures of exposure.

Biomarkers of Genetic Damage

Biomarkers can include measures of damage from specific chemical agents (for example, DNA adducts; Table I; Shugart and Kao, 1985; Martineau et al., 1988) or can be nonspecific indicators of damage to the integrity of DNA (such as numbers of strand breaks in the DNA; Fig. 2; Shugart, 1988; Shugart et al., 1989). Biomarkers of genetic damage can be considered equally applicable in assessing effects on plants and animals.

Induction of Detoxifying Systems as a Biomarker

Most contaminants stimulate synthesis of relatively specific protective detoxication mechanisms; higher levels of these proteins in organisms are evidence of a molecular response to toxicant exposure. Mixed-function oxidase system enzymes (Fig. 3; Jiminez et al., 1988; Loar, 1988), metal binding proteins (Table 2; Hamilton and Mehrle, 1986), and oxyradical-scavenging enzymes are examples of detoxification systems used as biomarkers.

Inhibition of Specific Enzymes or Biochemical Pathways

Exposure to pollutants that exert their toxic action by specific mechanisms, such as the neurotoxic effect of many pesticides, may be indicated by changes in the target biochemical activity.

Impairment of Immune System Function

Specific toxicants or the cumulative effects of multiple contaminants may reduce the capacity of the immune system to resist infection (Anderson and Roberson, 1989).

Impaired Organ or Tissue Function

Histopathological analyses can detect neoplastic, necrotic, or parasitic lesions. Impairment of physiological function can be evaluated by a number of assays, such as analyses of blood chemistry (Loar et al., 1988; Loar, 1988).

Impairment of Reproductive Competence

In an ecological context, the adverse effects of exposure on individuals may be of less concern than the consequences at the population level. Reproductive success is the key process linking (1) molecular and biochemical effects of toxicants within an individual (e.g., genetic damage or hormonal aberrations) and (2) the ecosystem-level effect. Levels of reproductive hormones or observations of atresia in

Table 2. Metal-binding proteins (MBP) in the livers of bluegill sunfish (*Lepomis macrochirus*) exposed to cadmium in the laboratory and in redbreast sunfish collected from streams contaminated with metals, including zinc. Fish were injected intraperitoneally with 2 mg Cd/kg body weight as CdCl₂ in 0.9% saline on each of three consecutive days and then sacrificed on day 6. Control fish were similarly injected with 0.9% saline (50uL/100 g body weight) on each of three consecutive days and sacrificed on day 6. White Oak Creek drains the southern boundary of the Oak Ridge National Laboratory and flows into White Oak Lake. Brushy Fork Creek is used as a reference site because it has no inputs of industrial or other point source pollutants. MBP concentrations in livers were measured by the use of the Chelex-100/¹⁰⁹Cd procedure [Sloop, et al., 1989], and are reported as nanomoles of ¹⁰⁹Cd bound per gram of soluble protein ± S.E. M. The asterisk indicates that MBP concentrations are significantly different from those in control or reference animals at alpha = 0.05.

Sample description	MBP concentration
Laboratory Exposure (Cd)	
Control	247 ± 168 (n = 4)
Exposed	977 ± 133 (n = 3)*
Field Collection	
Reference Stream (Brushy Fork Creek)	631 ± 121 (n = 4)
White Oak Creek (3.0-3.4 km)	1900 ± 306 (n = 10)*
White Oak Creek (2.5 km)	1732 ± 368 (n = 6)*
White Oak Lake	1472 ± 404 (n = 4)*

developing oocytes may be useful biomarkers that can be linked to toxic agents, whereas observations of oocyte recruitment or other measures of reproductive competence can help quantify the consequences of pollutant exposure.

Interpretation of Biomarker Responses:
Levels of Biological Organization

The effects of environmental contamination can span a range of levels of biological organization, from the molecular level to the community level. Responses at each level provide information that help researchers to understand and interpret biomarker responses.

Exposure Versus Effects

The lower levels of organization, such as DNA damage or enzyme activity, often provide a more sensitive and specific response to par-

ticular toxicants. These biomarkers offer advantages as more direct measures of exposure and may be diagnostic of the type of contaminant to which the organism is exposed. However, it is less clear what the biological significance of that exposure might be to the overall structure and function of an ecosystem.

On the other hand, responses at higher levels of biological organization, such as changes in species diversity, provide a much more direct indication of ecosystem-level effects, but cannot by themselves prove whether the effect results from pollutants or from natural ecological factors. Some measures of toxic effect, such as reproductive competence, can be considered to be both biomarkers that can be more directly tied to toxic exposure and indicators of the population-level consequences of that exposure.

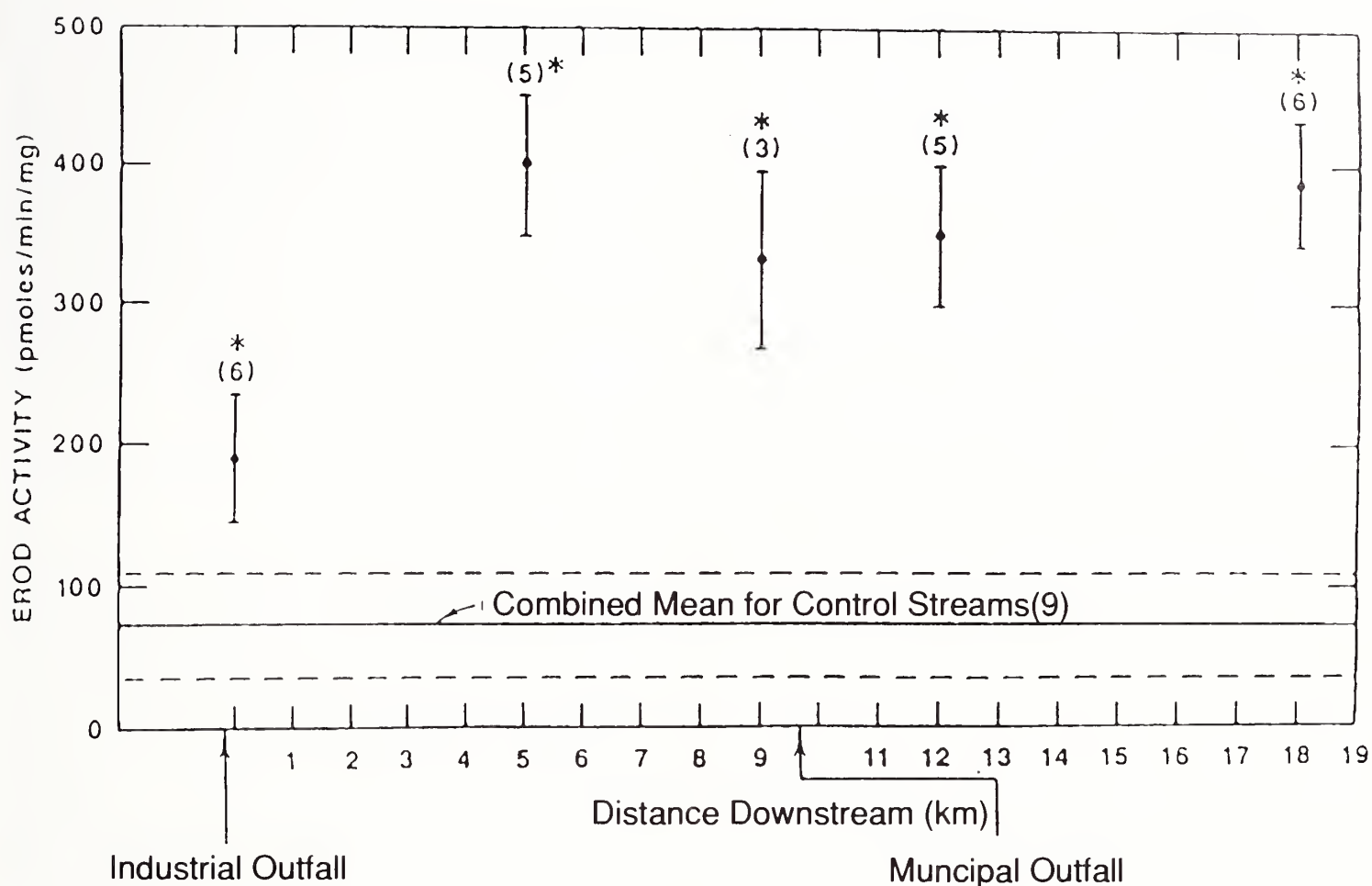


Figure 3. Induction of detoxication enzymes in fish. Fish in a stream contaminated by industrial effluents demonstrate significantly higher levels of a detoxication system, the mixed-function oxidase system. The levels of one enzyme activity of this system, ethoxyresofurin-O-deethylase (EROD), is measured in hepatic microsomes of bluegill sunfish collected in East Fork Poplar Creek (Oak Ridge, Tennessee) at different distances downstream from an industrial source (New Hope Pond) and compared to EROD levels in fish collected at the same time from Brushy Fork Creek, an unpolluted reference stream. Each point represents the mean \pm S.E.M. (n) for each station. Significant differences ($P < 0.01$) between the combined mean (-----) \pm SEM (_____) for the reference stream ("control stream") and for the stations in the stream receiving the industrial effluents are indicated by asterisks (see Jiminez et al., 1988).

A comprehensive and integrated monitoring program needs to consider responses at several levels of organization, using biomarkers at the organismic or suborganismic level, as well as indicators at the population and community levels, to answer the two critical questions that motivate this activity.

1. Are organisms exposed to levels of toxicants that exceed the capacity of normal detoxication and repair systems?
2. If there is evidence of exposure, then does the pollutant stress have an impact upon

the structure and function of the ecosystem?

Short-term predictors of long-term ecological effects

The ultimate goal of an environmental monitoring program is to prevent deterioration of the environment and to document recovery of affected systems. Biomarkers at the molecular and biochemical level respond quickly to changes in contaminant exposure, whereas a long latent period may be required before any change is apparent at a community level or

ecosystem level. Can these rapidly responding biochemical level markers serve as short-term predictors of long-term effects? We cannot yet make any links with any confidence. However, the data base derived from an environmental monitoring program will clarify the relationships between the response of the biochemical markers to an exposure and the eventual ecological consequences of that exposure. The ultimate goal would be the establishment of a scientifically defensible basis for predicting ecosystem-level consequences through the use of cost-effective, timely measures of biomarker responses in exposed individuals.

Validation of Biomarkers of Environmental Contamination

Monitoring biomarkers in environmental species presents numerous advantages for assessing the amount and significance of exposure to hazardous pollutants. However, the approach will require the development of an extensive body of data and testing in a wide variety of sites for the significance of the biomarker responses to be understood and for the full power of their predictive capabilities to be applied with confidence. In spite of the hurdles, there are few reasonable alternatives that can provide information needed to understand the complex interactions of chemical toxicants in the environment. The ultimate validation of the biomarker concept will require an iterative interaction between three crucial elements.

Field Studies

Field studies are the core of the environmental monitoring program. A stable monitoring effort will provide data on biomarker responses in pristine areas and polluted areas so that exposure differences both between sites and over time can be evaluated. Care must be exercised in interpreting and accounting for "noise" in biomarker responses that results from ecological and biological complexities of the real world.

Laboratory Studies

Field studies provide only correlations; ecological complexities and other factors make it difficult to use field data to establish dose-dependent causal relationships between exposure and biomarker responses. Laboratory research is necessary to establish these relationships and to unravel and document the shifts in biomarker response that result from environmental variables, such as seasonal changes in temperature, or from hormonal effects during reproductive cycles.

Fundamental Toxicological Understanding of Biomarker Responses

Selection of the biomarkers used in the monitoring program must be justified on the basis of a fundamental understanding of the molecular, biochemical, and higher level interactions linking exposure, biomarker responses, and ultimate adverse effects at individual, population, and community levels. Future advances in the basic toxicology underlying the biomarker responses will strengthen and validate the acceptance of biomarker responses as a scientifically and legally defensible methodology for evaluating and remediating environmental pollution.

Eventual success in applying and interpreting biomarkers will require a continuing interaction between these three elements: field studies will raise questions that must be resolved in laboratory experiments; the results of the experiments will enhance our understanding of the fundamental toxicology and biochemistry of the biomarker response; these new insights will improve our ability to interpret the field results and refine additional hypotheses to be tested in the lab and field.

Status of Current Capabilities and Future Directions

Biomarkers in all the categories or levels of biological organization, listed in the section

entitled "Selection of a suite of biomarkers," have been demonstrated in at least some laboratory and field experiments (e.g., see McCarthy et al., 1989). Much of this research has been limited to either (1) laboratory exposures of animals to a limited number of well-described model contaminants or (2) measurements of a single biomarker response in field-collected animals. However, a handful of research groups have collaborated to evaluate the responses of a suite of biomarkers in animals from polluted environments. The results have been encouraging: biomarker responses have correlated with the perceived degree of contamination, and the relative ranking of sites on the basis of molecular and biochemical responses agrees well with community level measures of ecosystem integrity (Loar et al., 1988; Loar, 1988). However, the same biomarkers have not been used in all the studies, repeated monitoring at the same sites is rare, and large-scale field studies have been limited almost exclusively to marine or aquatic environments.

Nevertheless, core capabilities for measuring a fairly wide array of candidate biomarkers do exist at federal agencies, national laboratories, and universities, and sufficient experience exists for making rational choices about selection and sampling of animal species. The primary impediments to major progress in applying this approach to environmental monitoring is the lack of a unifying mandate and the need for stable long-term funding. Concern about ensuring the quality of the environment transcends national boundaries. International symposia such as this are critical to achieving the consensus necessary to organize and coordinate long-term and comprehensive monitoring programs that include the use of sensitive and powerful biomarkers in sentinel species as tools to document exposure to, and effects of, environmental contamination.

Literature Cited

- Adams, S.M., and B.D. Jimenez. 1987. Biological indicators of contaminant-related stress. In Loar, J.M. (ed.), *First Annual Report on the ORNL Biological Monitoring and Abatement Program*. ORNL/TM-10399, Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Anderson, D.P., and B.S. Roberson. 1989. Immunological indicators: Effects of environmental stress on immune protection and disease outbreaks. In S.M. Adams (ed.), *Biological Indicators of Stress in Fish*. American Fisheries Society Symposium Publication, Bethesda, Md. (in press).
- Hamilton, S.J., and P.M. Mehrle. 1986. Metallothionein in fish: review of its importance in assessing stress from metal contaminants. *Trans. Am. Fish. Soc.* 115:596-609.
- Jimenez, B.D., L.S. Burtis, G.H. Ezell, B.Z. Egan, N.E. Lee, J.J. Beauchamp and J.F. McCarthy. 1988. Effects of environmental variables on the mixed function oxidase (MFO) system in bluegill sunfish (*Lepomis macrochirus*). *Environ. Toxicol. Chem.* 7:623-634.
- Loar, J.M. (ed.). 1988. *Second annual report on the ORNL Biological Monitoring and Abatement Program*. ORNL/TM. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Loar, J.M., S.M. Adams, H.L. Boston, B.D. Jimenez, J.F. McCarthy, J.G. Smith, G.R. Southworth, and A.J. Stewart. 1988. *First annual report on the Y-12 Plant Biological Monitoring and Abatement Program*. ORNL/TM. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Martineau, D., A. Lagace, P. Beland, R. Higgins, D. Armstrong, and L.R. Shugart. 1988. Pathology of stranded beluga whales (*Delphinapterus leucas*) from the St. Lawrence estuary, Quebec, Canada. *J. Comp. Pathol.* 98:287-311.
- McCarthy, J.F., L.R. Shugart, and B.D. Jimenez. 1989. Biological markers in wild animal sentinels as predictors of ecological and human health effects from environmental contamination. In C.W. Gehrs (ed.), *Eighth Life Science Symposium on Bioindicators: Exposure and Effects*. Oak Ridge National Laboratory, Oak Ridge, Tenn. (in press)
- National Research Council. 1986. Committee on Biological Markers. Washington, D.C.

- Shugart, L.R. 1988. Quantitation of chemically induced damage to DNA of aquatic organisms by alkaline unwinding assay. *Aquat. Toxicol.* (in press).
- Shugart, L.R., and J. Kao. 1985. Examination of adduct formation *in vivo* in the mouse between BaP and DNA of skin and hemoglobin of red blood cells. *Environ. Health Perspect.* 62:223-226.
- Shugart, L.R., J. McCarthy, B. Jimenez, and J. Daniels. 1987. Analysis of adduct formation in bluegill sunfish (*Lepomis macrochirus*) between benzo[a]pyrene and DNA of the liver and hemoglobin of the erythrocyte. *Aquat. Toxicol.* 9:319-325.
- Shugart, L.R., J.M. Holland, and R. Rahn. 1983. Dosimetry of PAH skin carcinogenesis: Covalent binding of benzo[a]pyrene to mouse epidermal DNA. *Carcinogenesis* 4:195-199.
- Shugart, L.R., S.M. Adams, B.D. Jimenez, S.S. Talmage, and J.F. McCarthy. 1989. Biological markers in animals can provide information on exposure and bioavailability of environmental contaminants. In Wang, R., and C. Franklin (eds.), *Chemical Basis for Biological Monitoring*. American Chemical Society Symposium Series, Washington, D.C. (in press).
- Sloop, F.V., L.R. Shugart, J.F. McCarthy, and K.B. Jacobson. 1989. An assay for metallothionein using Chelex-100 and cadmium-109. *Anal. Biochem.* (in press).

Comparative Estimates of the Effects of Ozone, Sulphur Dioxide and Nitrogen Dioxide on Plant Productivity

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Atmospheric pollution by industrial emissions in the recent two decades has spread beyond local boundaries, and now inflicts significant ecological and economic effect on the state of terrestrial plant cover on regional and global scales (Guderian, 1985; Treshow, 1985; Izrael, 1986).

Agricultural crop damage in the U.S., for example, due to the atmosphere pollution in 1981, made up 1.7 billion US \$ (Treshow, 1985). The problem gave impetus to physiological and ecological research on biological effects of pollution and ecological standard setting (Rachkovskaya, 1986; Guderian, 1985; Treshow, 1985; Izrael, 1986).

Of particular interest among atmospheric pollutants are SO_2 , NO_2 and O_3 , since the former two are characteristic components of industrial emissions. They are fairly persistent, phytotoxic, and might be transported in the atmosphere over long distances (~1000 km). Ozone, also phytotoxic, originates in the troposphere in the course of photochemical reactions involving nitrogen oxide and hydrocarbons.

To investigate the effect of atmospheric pollution on plant productivity, many scientists (A. S. Heagle, W. Heck, J. H. Bennet, V. S.

Runeckles, J. M. Skelly, L. W. Kress, K. M. Niomarkay, and others) set up and implemented laboratory and field experiments, observing plants in special chambers. Plant seeds and seedlings, or cuttings were used, and they were grown in chambers in controlled environments with prescribed levels of pollution (varying or constant). By the end of an experiment, the biomass (B) of a plant, or of its parts (above- or under- ground), or the yield were measured.

I. M. Kunin (1986 and 1988) has arranged the published data on the experiment results into standardized data sets:

$$D_{i1}^k < D_{i2}^k < \dots < D_{in_i}^k$$
$$B_{i1}^k, B_{i2}^k, \dots, B_{in_i}^k$$

where, i is the experiment number, n_i is the number of pollution levels in the given experiment, and D_{ij} and B_{ij} , dose and effect, respectively. The data sets are grouped into data files, set numbers within a data file being independent; index k refers the data sets to respective data files. Each data file implies the pollutant (SO_2 , NO_2 , or O_3), examined indicator (total biomass of a plant, of its parts, or yield), and plant group under study (agricultural crops, trees). Data on the effect of long-term exposure (during a growing season, or longer) to low pollutant

concentrations (usually < 0.1 ppm) have been analyzed; this is relevant to background regional and global problems.

When analyzing this information, A. H. Ostromoguisky (1988) obtained mathematical expectation (mean value) for the parameters of dual-parameter “dose-effect” model. Applying the method suggested by F. N. Semevsky, I. M. Kunina (1987) examined the difference of plant responses to ozone during various phases of ontogenesis. The difference was insignificant by the statistical criterion.

In this paper, comparative analysis of average sensitivity of the mentioned groups of plants to SO₂, NO₂ and O₃ is discussed, and the method for computing changes in annual production of higher plants exposed to the pollutant impact is suggested.

The above mentioned files of ecological information have been analyzed by a single-parameter model:

$$\ln B_{ij}^k = a_i^k - \zeta^k D_{ij}^k + \xi_{ij}^k$$

where, a_i^k is mathematical expectation of the

measured indicator (logarithm scale) for the i -th set in the k -th file under no pollution, ζ^k – sensitivity of the group of plants in the k -th file to the respective pollutant with respect to related biological indicator, ξ_{ij}^k – random fluctuations, i.e. independent realizations of random value ξ^k , individual for each data file. Value $\hat{\zeta}_i^k$ of parameter ζ^k is computed for each i -th data set within the k -th data file by means of the linear regression method as follows:

$$\hat{\zeta}_i^k = \zeta^k + \frac{\theta_i^k}{W_i^k},$$

$$(W_i^k)^2 = \sum_{j=1}^{n_i^k} (D_{ij}^k)^2 - n_i^k \left(\frac{\sum_{j=1}^{n_i^k} D_{ij}^k}{n_i^k} \right)^2; i = 1, \dots, m_k$$

where, m_k – the number of data sets within the k -th data file, $\theta_1^k, \dots, \theta_{m_k}^k$ – independent realizations of the random value θ^k whose variance equals variance ξ^k .

Further, the virtual value $\bar{\zeta}^k$ of parameter ζ^k and its error $\varsigma_{\bar{\zeta}^k}$ are defined by formulae:

Table 1. Estimates of the sensitivity parameter ζ of higher plants to pollutant impact

Data file number, k	Pollutant	Estimate of $\zeta^k, \bar{\zeta}^k$	Estimate of error $\varsigma_{\bar{\zeta}^k}$	Number of data sets in a file m_k
Agricultural crops (total biomass)				
1	NO ₂	1.2	0.3	65
2	SO ₂	1.6	0.2	199
3	O ₃	15.5	1.1	116
Agricultural crops (yield)				
4	O ₃	11.3	1.3	56
Agricultural crops (root biomass)				
5	SO ₂	2.1	0.4	70
Trees (total biomass)				
6	NO ₂	0.2	0.2	24
7	SO ₂	0.7	0.2	43
8	O ₃	5.8	1.1	37

$$\bar{\zeta}^k = \sum_{i=1}^{m_k} \lambda_i^k \zeta_i^k; \zeta_{\bar{\zeta}}^k = \sqrt{\frac{\sum_{i=1}^{m_k} \lambda_i^k (\zeta_i^k - \bar{\zeta}^k)^2}{m_k - 1}}$$

where

$$\lambda_i^k = \frac{(w_i^k)^2}{\sum_{l=1}^{m_k} (w_l^k)^2}$$

– optimum weight coefficients. Computation results are given in Table 1; the measurement units for $\bar{\zeta}$ and $\zeta_{\bar{\zeta}}$ are in $10^{-3} \text{ ppm}^{-1} \text{ hour}^{-1}$.

To specify the error distribution, empiric distribution of

$$\theta_i^k = (\zeta_i^k - \bar{\zeta}^k) w_i^k$$

normalized with respect to their standard deviations has been derived (Fig. 1). Verification of the difference of these distributions from standard normal by statistical criterion has produced a negative result.

The defined parameters can be used to make assessments (averaged for the globe or regions) for controlling plant production during the growing season:

$$P = P_0 \exp\left(-\zeta_{(\text{SO}_2)} \Delta D_{(\text{SO}_2)} - \zeta_{(\text{NO}_2)} \Delta D_{(\text{NO}_2)} - \zeta_{(\text{O}_3)} \Delta D_{(\text{O}_3)}\right) \quad (1)$$

Here, P_0 and P —the initial and altered values of the productivity index, respectively, $\Delta D_{(.)}$ —change in the pollutant dose, $\zeta_{(.)}$ —the parameter which is characteristic of the respective group of plants, the acting pollutant, and production index (Table 1). Formula (1) is based on the assumption of an independent effect of the pollutants under consideration since our analysis of the published data on the effect of SO_2 , NO_2 and O_3 in combination with the considered indicator has revealed no reliable difference between the combined effect (averaged with respect to relevant plant groups) and the additive effect (Izrael, 1988).

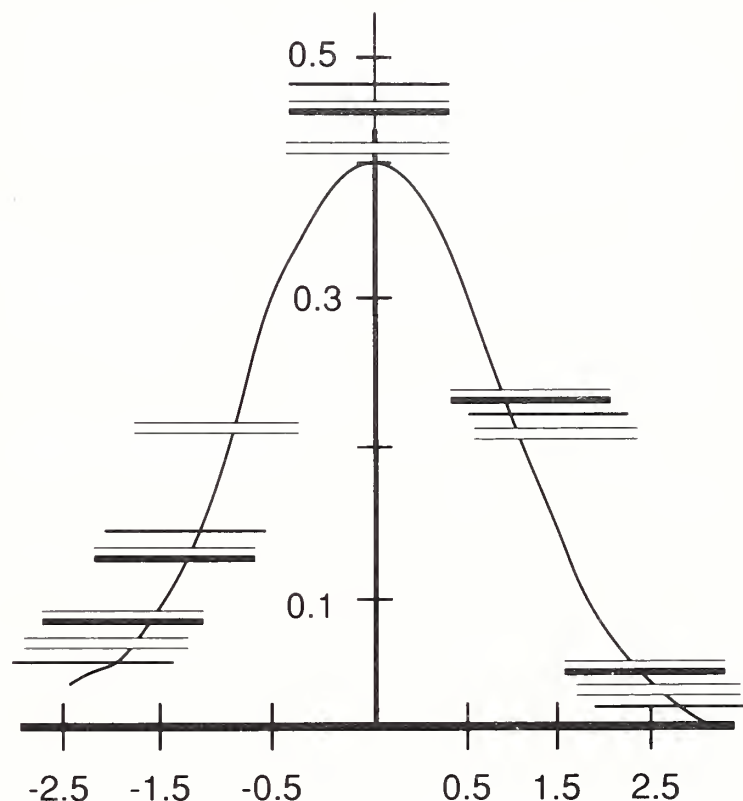


Figure 1. Empiric distributions of random fluctuations θ_i^k for the effects on total biomass of agricultural crops: O_3 (.....), NO_2 (—), SO_4 (——) and standard normal distribution

So, to characterize higher plant sensitivity to pollutant impact, we have applied parameter ζ which implies a relative change in plant biomass (productivity) per unit increase in pollution dose. The effect of SO_2 , NO_2 and O_3 on all the considered indices of the state of a plant through

photosynthesizing organs is confidently adverse (here and further on the confidence level being over 90%), i.e. $\zeta < 0$, except NO_2 effect on the total tree biomass (neutral). In terms of the impact on the total plant biomass (both for trees and agricultural crops) $\text{O}_3 > \text{SO}_2, \text{NO}_2$, and for trees, $\text{SO}_2 > \text{NO}_2$ ($>$ implies "more phytotoxic"). On the average, trees are less sensitive to each of the considered pollutants than agricultural crops; ozone effect on the crop yield is lower than on the total biomass. Sulphur dioxide effect on roots biomass of agricultural crops is higher than on the total biomass (the confidence level is over 85 %).

Estimates of parameters ζ^k (Table 1) can be used for assessing changes in the annual production of higher plants exposed to background regional and global levels of SO_2 , NO_2 and O_3 (Formula(1)).

In view of a high priority of ozone as of a phytotoxic pollutant, it is necessary to develop quantitative methods for ozone flux studies, to develop the ozonometer station network, to develop actions for reducing man-induced levels of ozone in the troposphere.

Literature Cited

- Effects of SO_2 on Plants. Moscow, Gidrometeoizdat, 1984.
- Guderian, R., (ed.). 1985. *Air Pollution by Photochemical Oxidants*. Springer-Verlag, Berlin, Heidelberg, New-York, Tokyo.
- Izrael Yu. A., and S.M. Semjenov . 1986. Ecological horizon. *In Acidification and its Policy Implications*. Elsevier, Amsterdam.
- Izrael Yu. A., S.M. Semjenov, and I.M. Kunina. 1988. Integrated approach to ecological Standard setting for air pollution. *In Problems of Ecological Monitoring and Ecosystem Modelling*. L., Gidrometeoizdat, v.11.
- Izrael Yu. A. 1984. *Ecology and Control of the State of the Natural Environment*. L., Gidrometeoizdat, 1984.
- Kullina I. M. 1987. Assessment of ozone effect on plant phytomass and yield. *In Problems of Ecological Monitoring and Ecosystem Modelling*. L., Gidrometeoizdat, v. 10.
- Kunina I. M. 1986. Ozone effect of plants. *In Problems of Ecological Monitoring and Ecosystem Modelling*. L., Gidrometeoizdat, v.9, p.44-87.
- Kunina I. M. 1988. *The effect of O_3 , NO_3 , NO_2 , SO_2 on higher plant biomass*. Obninsk, VNIIGMI-WDC.
- Nikolayevky, V.S. 1980. *Gas-resistance of plants*. Novosibirsk, Nauka.
- Ostromoguilsky, A.H., and I.M. Kunina. 1988. Quantitative patterns of the effect of O_3 , SO_2 , and NO_2 on higher plants. *In Problems of Ecological Monitoring and Ecosystem Modelling*. L., Gidrometeoizdat, v.11.
- Rachkovskaya M.M. 1986. The principles of ecological standard setting by functional criteria. *In Problems of Ecological Monitoring and Ecosystem Modelling*. L., Gidrometeoizdat, v.9,.
- Treshow, M. (ed.). 1985. *Air Pollution and Plant Life*, John Wiley & Sons.

Indigenous and Cultivated Plants as Bioindicators of Air Pollution Injury

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Many species of plants are extremely sensitive to some of the most important air pollutants. For example, in some cases, such as with airborne gaseous fluorides, certain species of plants may be more sensitive than man by more than three orders of magnitude (less than $1 \mu\text{g m}^{-3}$ for injury to gladiolus, goatweed [*Hypericum perforatum*], redbud [*Cercis canadensis*], and other species, as compared with the OSHA standard of 3.5 mg m^{-3} for an 8-hr working day over a lifetime).

Because of the characteristic sensitivity of plants, and their ubiquity in forest, aquatic, and agroecosystems, selected indigenous and cultivated plants have been used for many years (e.g., Ruston, 1921) to study air pollution problems (Benedict and Breen, 1955; Berge, 1973; Brandt and Heck, 1968; Cole, 1958; Darley, 1960; Feder, 1978; Heck, 1966; Heck et al., 1966; Heck and Heagle, 1970; Heggestad and Menser, 1962; Hepting, 1966; Jacobson, 1977; Jacobson and Hill, 1970; Kromroy et al., 1988; Leone et al., 1964; Mellanby, 1978; Nakamura and Matsunaka, 1974; Nouchi and Aoki, 1979; Oshima, 1974; Posthumus, 1976; Scholl, 1971; Thomas, 1951; Thomas, 1961; Treshow, 1965; van Raay, 1969; Weinstein, 1977; Weinstein and Laurence, 1988; Zimmerman and Hitch-

cock, 1956). There are many potential uses of plants as pollutant indicators or monitors: (a) establishing the presence of a pollutant, (b) providing an early warning system for certain air pollutants, (c) relating dose to response (in a general way only), (d) delineating the spatial and temporal distribution of a pollutant, (e) aiding in identification of pollutants, and (f) measuring pollutant accumulation to conform to a standard that protects plants and/or animals.

To be useful, these bioindicators must be (a) genetically uniform to minimize natural variability (Feder, 1978; Feder and Manning, 1979), (b) sensitive to a specific pollutant so that characteristic and recognizable symptoms are produced, (c) abundant and widely distributed (Darley, 1960), (d) able to maintain growth over the entire growing season (Heck, 1966), and (e) capable of absorbing a pollutant in a predictable manner if it is to be used as a measure of accumulation (Feder, 1978; Feder and Manning, 1979; Guderian, 1977).

Plants may respond to air pollutants by displaying (a) characteristic chlorotic or necrotic lesions, generally on foliage or fruits; (b) changes in pigmentation, such as destruction of existing or inhibition of *de novo* chlorophyll

synthesis, or excessive anthocyanin production; (c) alteration of form; each of these are due to (d) alteration in metabolism. Many of these responses are more easily and less expensively measured than the usual physical or chemical detection of pollutants. Furthermore, the plant, unlike instruments, integrate the effects of toxicants over a wide range of environments (Heck et al., 1966; Thomas, 1961; Treshow, 1965). Thus, in this context, they are biointegrators, expressing the biological effect of a pollutant dose, and integrating climatic, cultural, and other biological factors into their response by being "tuned" to the ecosystem. Disadvantages of plants as bioindicators are that susceptible species may not be distributed over the area of concern, and that they provide information after-the-fact (as compared with instruments that operate by chemical or physical principles).

Not all plants are sensitive to air pollutants. Often, there is a significant range in sensitivities among cultivars of the same species. Extremely tolerant species or cultivars are valuable for planting on farms and in cities near pollution sources. Tolerant species may also be good accumulators of pollutants, and can play a special role in programs to monitor pollution over a geographical area. For example, in Ontario, the accumulation of fluoride in leaves of silver maple, a common indigenous tree species of only moderate sensitivity, is used to judge the degree of pollution in a specific area. Concentrations of fluoride above a certain value indicate a polluted condition. Similarly concentrations of fluoride in forage may be used as an indicator of potential health problems with suspect to grazing animals.

In areas where sensitive species of indigenous or cultivated plants are not present or widely distributed, a number of field monitoring systems have been devised and are in use in various countries. Several are briefly described below.

Indicator gardens

These gardens consist of plants that are selected for their sensitivity to pollutants known or suspected to occur (Anonymous, 1984; Arndt et al., 1987; Feder, 1978; Feder and Manning, 1979; Kromroy et al., 1988; Posthumus, 1976; van Raay, 1969). The State of Minnesota has used indicator gardens to monitor the presence of sulfur dioxide and ozone in phytotoxic concentrations (Anonymous, 1984; Kromroy et al., 1988). Plants in indicator gardens are grown in a standardized soil or artificial soil mix, using proscribed cultural methods.

Portable exposure benches

This technique is used extensively in Europe for the culture of sensitive trees and crops (Arndt et al., 1985; Arndt et al., 1987). The exposure bench provides a means of automatic care for plants grown in isolated areas where frequent visits are difficult or become too expensive. The exposure bench not only supports indicator plants above the ground for protection from animals, but also provides an automatic watering system.

Grass culture

Standard methods for the use of ryegrass cultures have been devised for detecting the presence of certain pollutants and measuring their rates of deposition (Arndt et al., 1987; Scholl, 1971). Grass cultures have been used to measure fluoride, sulfur, chloride, lead, cadmium, zinc, copper, nickel, vanadium, etc. The typical grass culture consists of a container with a defined medium to support the growth of ryegrass plants, an automatic water supply, and a post that supports the unit at a specific distance above the ground. The grass is harvested and analyzed periodically to determine the presence and concentration of toxic elements, the rate of uptake, and total accumulation.

Many variations of these basic methods have been devised, including the use of lichen transplants (which will not be discussed here). The use of higher and lower plants for biomonitoring offers several advantages over instruments based upon physical-chemical techniques. Not the least of these are low cost, potential to determine pollutant dispersion over wide geographical areas, and an approximation of source strength.

Literature Cited

- Anonymous. 1984. *Development of a Biological Air Quality Indexing System*. A Report to the Minnesota Air Quality Board. 380 pp. St. Paul, MN 55101.
- Arndt, U., W. Erhardt, A. Keitel, K. Michenfelder, W. Nobel, and C. Schluter. 1985. Standardisierte Exposition von pflanzlichen Reaktionsindikatoren. *Staub-Reinh. Luft* 45:481-483.
- Arndt, U., W. Nobel, and B. Schweizer. 1987. *Bioindikatoren. Möglichkeiten, Grenzen und neue Erkenntnisse*. 388 pp. Eugen Ulmer GmbH & Co., Stuttgart, FRG.
- Benedict, H.M., and W.H. Breen. 1955. *The use of weeds as a means of evaluating vegetation damage caused by air pollution*. Proc. Natl. Air Pollution Symp., 3rd, pp. 177-190.
- Berge, H. 1973. Plants as indicators of air pollution. *Toxicology* 1:79-89.
- Brandt, C.S., and W.W. Heck. 1968. Use of plants for pollutant identification and field monitoring. pp. 428-443. In A.C. Stern (ed.) *Air Pollution, Vol. 1*, 2nd ed. Academic Press, New York.
- Cole, G.A. 1958. Air pollution with relation to agronomic crops. III. Vegetation survey methods in air pollution studies. *Agron J.* 50:553-555.
- Darley, E.F. 1960. Use of plants for air pollution monitoring. *J. Air Pollut. Control Assoc.* 10:198-199.
- Feder, W.A. 1978. Plants as bioassay systems for monitoring atmospheric pollutants. *Environ. Health Perspect.* 27:139-147.
- Feder, W.A., and W.J. Manning. 1979. Living plants as indicators and monitors. In W.W. Heck, S.V. Krupa, and S.N. Linzon, (eds). *Handbook of Methodology for the Assessment of Air Pollution Effects on Vegetation*. TE-2 Agricultural Committee, Air Pollution Control Association, Pittsburgh, PA.
- Guderian, R. 1977. Air pollution: Phytotoxicity of acidic gases and its significance in air pollution control. Chapter 4 In *Ecological Studies, Vol. 22*, Springer-Verlag, Berlin.
- Heck, W.W. 1966. The use of plants as indicators of air pollution. *Air Water Pollut.* 10:99-111.
- Heck, W.W., J.A. Dunning, and I.J. Hindawi. 1966. Ozone: Nonlinear relation of dose and injury in plants. *Science* 151:577- 578.
- Heck, W.W., and A.S. Heagle. 1970. Measurement of photochemical air pollution with a sensitive monitoring plant. *J. Air Pollut. Control Assoc.* 20:97-99.
- Heggstad, H.E., and H.A. Menser. 1962. Leaf spot-sensitive tobacco strain Bel-W3, a biological indicator of the air pollutant ozone. *Phytopathol.* 52:735.
- Hepting, G.H. 1966. Air pollution impacts to some important species of pine. *J. Air Pollut. Control Assoc.* 16:63-65.
- Jacobson, J.S. 1977. Plants as indicators of photochemical oxidants in the U.S.A. *VDI-Berichte Nr.* 270:191-196.
- Jacobson, J.S., and A.C. Hill. (eds.) 1970. *Recognition of air pollution injury to vegetation: A pictorial atlas*. Air Pollution Control Association, Pittsburgh, PA. 102 pp.
- Kromroy, K. W., P. S. Teng, M. Olson, D. French, and D. S. Lang. 1988. A biological system for indexing air quality and assessing vegetation effects (Minnesota Bioindicator Study). *Environ. Pollut.* (In press).
- Leone, I.A., E. Brennan, and R.H. Daines. 1964. *Plant life as air pollution indicators*. Proc. Northeast. Weed Control Conf. 18:451- 457.
- Lihnell, D. 1969. Sulphate contents of tree leaves as an indicator of SO₂ air pollution in industrial areas. pp. 341-352. In *Air Pollution, Proc. First European Congr. on Influence of Air Pollution on Plants and Animals*. Wageningen, 1968.

- Mellanby, K. 1978. Biological methods of environmental monitoring. pp. 1-13. In J. Lenihan and W.W. Fletcher, (eds). *Environment and Man, Vol. 7: Measuring and Monitoring the Environment*. Academic Press, New York.
- Nakamura, H., and S. Matsunaka. 1974. *Indicator plants for air pollutants. Susceptibility of morning glory to photochemical oxidants: Varietal difference and effect of environmental factors*. Proc. Crop Sci. Soc. Jpn. 43:522.
- Nouchi, I., and K. Aoki. 1979. Morning glory as a photochemical oxidant indicator. *Environ. Pollut.* 18:289-303.
- Oshima, R.J. 1974. A viable system of biological indicators for monitoring air pollutants. *J. Air Pollut. Control Assoc.* 24: 576-578.
- Posthumus, A.C. 1976. *The use of higher plants as indicators for air pollution in the Netherlands*. Proc. Kuopio Meeting on Plant Damages Caused by Air Pollution, Sci. Pap. Symp., 1976, pp. 115-120.
- Ruston, A.G. 1921. The plant as an index of smoke pollution. *Ann. Appl. Biol.* 7:390-403.
- Scholl, G. 1971. Die Immissionsrate von Fluor in Pflanzen als Masstab für eine Immissionsbegrenzung. VDI Berichte Nr. 164. pp. 39-45.
- Thomas, M.D. 1951. Gas damage to plants. *Annu. Rev. Plant Physiology* 2:293-322.
- Thomas, M.D. 1961. Effects of air pollution on plants. pp. 233-278. In *Air Pollution*. World Health Organization Monograph Series #46. Columbia University Press, New York.
- Treshow, M. 1965. Evaluation of vegetation injury as an air pollution criterion. *J. Air Pollut. Control Assoc.* 15:266-269.
- van Raay, A. 1969. The use of indicator plants to estimate air pollution by SO₂ and HF. pp. 319-335. In *Air Pollution*. Proc. First European Congr. on the Influence of Air Pollution on Plants and Animals, Wageningen, 1968.
- Weinstein, L.H. 1977. Fluoride and plant life. *J. Occup. Med.* 19:49-78.
- Weinstein, L.H., and J.A. Laurence. 1988. *Indigenous and cultivated plants as biomonitors*. NRC Symp. on Biomonitoring. In press.
- Zimmerman, P.W., and A.E. Hitchcock. 1956. Susceptibility of plants to hydrofluoric acid and sulfur dioxide gases. *Contrib. Boyce Thompson Inst.* 18:263-279.

Element Accumulation in Lichens, Mosses and Soils Connected with Mud Volcano Activity

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It is well known that lichens are widely used as indicators of air pollution, and as tools for biogeochemical monitoring in impact and background areas (Martin, 1987).

As a pollution point source analog, the mud volcanos form dispersion zones around active gas release areas. However, principal differences of these pollution sources are connected with the time scale (thousands of years), number and concentration of elements emitted.

Natural and anthropogenic anomalous matter flow situations, both sharing similar scientific goals, led us to use lichens and mosses to estimate elements carried out and dispersed around the mud volcanos.

Mud volcanos are intensive background forming sources in the recent biosphere. As magmatic volcanos, they are situated in tectonically active areas of the East and West Pacific and Alpine-Himalaya stress zones. There are about 730 mud volcanos worldwide, and ap-

proximately half of them are situated on the territory of the U.S.S.R. (Kropotkin, Valyaev, 1981).

The main contributing factor of the mud volcanic activity is gas release. On the base of measurements made on the Azerbaidjan S.S.R. (Caucasus region) volcanos, it was estimated that the world carrying-out during mud gryphon activity and eruptions is 10^6 - 10^7 tons of gas and 10^7 - 10^8 tons of breccia annually (Alexeyev, Alexeyeva, 1985).

Four active mud volcanos, Voskhod, Bulganakhsy, Shugo and Jau-Tepe, belonging morphologically to various types, were investigated in the Black Sea region, Kerch peninsula of Crimea and Tamansky peninsula.

Metal content in fine particles in snow cover was estimated by using x-ray fluorescent analysis, where soil and plant material samples were analysed using the neutron activation technique. The sample size used for radiation in block-containers was 100 mg per sample.

Botanical field materials were collected in April, 1987. On the slopes of the cone-shaped mud volcano, Voskhod, approximately 30 m from the top, sample plots were established radially. Collected plant samples included the lichens, *Cladonia convoluta* (Lam.) P. Cout., *Cladonia rangiformis* Hoffm., *C. furcata* (Huds.) Shard., mosses, *Tortula ruralis* (Hedw.) Gard. and *Homalothecium lutescens* (Hedw.) B.S.G. Corresponding soil samples were taken from the 2cm surface layer.

The Shugo volcano has a depression about 100 m in diameter which is surrounded by 30-40 m high swell. Mixed samples of epiphytic lichens (*Parmelia acetabulum*, *P. quernica*, *Physconia pulverulenta* and *Xanthoria parietina*) growing on the trunks of the oak *Quercus robur* were collected from two opposite sides of the swell. The tree bark and living leaves as well as the soil-like material under the epiphytes were also collected.

The Bulganakhsky mud volcano has a large flat hollow surrounded by a 30 m high swell. The epigeic lichens, *Cladonia convoluta*,

C.rangiformis, *C. furcata* and corresponding soil samples were collected from flat mud surface and from the swell slopes on various distances from the center of mud field.

Results and Discussion

One of the ways to establish the role of the particles in the carrying out process is the comparison of metal content of the snow cover in the cracks and the snow outside of the cracks zone.

The average content of the fine fraction (size of particles: 0.2-4.0 microns) in snow samples from the cracks zone was 1 g per liter of snow water. Outside of this zone, the fine particles content in the snow was 0.01 g per liter. The contribution of fine fraction particles in the snow of the cracks zone was 73.3% on Voskhod volcano. Consequently, the fine fraction plays an essential role in the transport of metals such as Zn, Cu, As, Br, Pb, Fe.

On the basis of the actual concentrations of elements in samples and their average content in the earth's crust, the enrichment factors

Table 1. Element concentrations in the snow aerosols, enrichment factors and calculated outflow on the Bulganakhsky volcano, Kerch peninsula, Crimea.

Elements	Concentrations, ug l ⁻¹		Enrichment factors		Outflow	
	Large Fraction >4.0	Fine Fraction 4.0-0.2	L. fract.	F. fract.	kg/day	kg/year
K	414	349	0.8	0.4	70	25500
Ca	491	262	0.8	0.2	70	25500
Ti	139	149	1.5	0.9	26	9500
Fe	956	1773			250	91400
Cu	11.4	60.5	12	34	6.6	2420
Zn	14.8	95.3	9	30	10.2	3700
Ye	1.2	6.9	41	1300	0.7	260
As	1.3	23.3	38	360	2.2	800
Br	7.3	17.5	170	220	2.3	840
Pb	7.9	59	24	96	6.1	2200
Rb	4.4	9.5	1.4	1.7	1.1	400
Sr	12.4	18.7	1.8	1.5	2.8	1000
Y	1.7	5	2.9	4.5	0.7	260
Zr	8	8.5	2.3	1.3	1.5	550
Nb	1.7	2.3	4.1	32	0.4	150

(K_E) were calculated as the ratio of the element concentration in the sample to the iron concentration in the same sample using the following formula :

$$K_E = \frac{\frac{C_i}{C_{Fe}}}{\frac{K_i}{K_{Fe}}}$$

where C_i , C_{Fe} are actual concentrations of the elements in the samples, and K_i , K_{Fe} , the average contents of those elements in the earth's crust.

The calculated enrichment factors may be divided into two groups according to the factors value :

1. The first group includes K, Ca, Ti, Sr, Zr; these elements' behaviors are similar to iron whose enrichment factors are close to 1.
2. The second group includes Zn, Cu, Ye, As, Br, Pb; enrichment factors for these are within the range $10^1 - 10^3$, which means that noticeable enrichment has taken place.

It is important to point out that the enrich-

ment factors for the fine fraction are higher by an order of magnitude than that for the large fractions (particle's size over 4.0 microns).

The basic data on aerosols for the Bulgakovsky volcano and the calculated outflow are given in table 1.

Actual concentrations of elements in analysed plant samples are given in table 2.

Literature Cited

Alexeyev V.A., Alexeyeva N.G. 1985. *On outcome of heavy metals in outgassing of Earth - Nuclear-Physical methods of analysis in monitoring of the environment*. Proc. of the 2-nd All-Union meeting. Riga, 1982. Leningrad. p.243-250. (In russian).

Kropotkin P.N., Valyaev B.M. 1981. Geodynamics of the mudvolcanic activities (in connection with oil and natural gas). In: *Geological and geochemical fundamentals of oil and gas search*. Kiev. p.148-178. (In russian).

Martin J. 1987. *Dynamics of lichen synusia and their biogeochemical role in extremal environmental conditions*. Sverdlovsk. 26 p. (In russian).

Table 2. Element concentration (ppm) in soils, lichens, mosses, tree bark and leaves on the mud field of Shugo volcano, Kerch peninsula, Crimea

Ele.	Coef.	Soils	Lichens	Mosses	Tree bark	Leaves
Na	102	7.35-12.17	2.21-13.7	0.71-1.95	1.09-4.99	0.67-1.12
K	103	2.03-4.11	1.52-7.07	3.94-6.21	1.31-2.46	12.0-16.9
Ca	104	13.1-16.4	1.14-2.65	1.33-1.94	2.09-3.8	0.44-0.72
Sc	1	8.93-16.1	0.49-1.28	1.39-7.64	0.24-0.79	0.22-0.03
Cr	101	5.95-9.4	-	1.29-5.57	-	-
Fe	104	2.64-5.04	-	4.11-24.4	-	-
Co	101	1.09-1.86	-	1.36-9.09	-	-
Zn	102	1.79-4.97	-	4.25-18.7	-	-
As	1	3.65-6.99	1.62-7.26	1.14-6.22	0.87-2.61	0.05-0.37
Se	10-1	7.22-18.9	2.59-7.67	0.85-23.7	0.27-4.05	0.80-2.10
Br	1	3.45-7.06	1.43-12.2	1.96-8.25	2.95-5.38	0.52-1.24
Ni	101	-	-	2.83-9.37	-	-
Rb	101	6.89-14.60	-	1.00-6.64	-	-
Mo	10-1	-	9.02-27.4	11.4-39.1	14.8-27.1	4.4-8.92
Ag	10-1	-	1.12-4.01	1.15-24.9	0.93-1.44	0.34-1.09
Cd	1	1.25-10.1	2.91-10.1	0.25-47.2	2.54-7.09	0.77-2.25
Te	1	6.05-12.2	-	-	-	-
Sb	10-1	32.1-81.3	3.33-7.90	0.99-3.77	2.17-4.22	0.31-0.49
Cs	10-1	21.6-55.5	1.25-5.30	0.66-0.25	0.82-3.21	0.02-0.23
Ba	101	31.0-65.0	1.15-8.32	6.14-17.3	389-1500	40.06-49.9
La	1	14.0-21.6	2.54-4.96	3.68-16.8	1.39-3.45	0.07-0.14
Ce	1	32.0-71.7	4.65-9.66	7.5-43.4	2.08-6.85	0.21-0.95
Sm	10-1	14.4-21.3	2.33-5.51	3.94-16.9	1.35-4.21	0.09-0.14
Eu	10-1	9.45-21.0	0.98-2.39	2.01-11.1	0.04-1.51	0.008-0.03
Tb	10-1	4.57-10.9	0.66-1.66	1.51-8.05	0.39-1.04	0.01-0.11
Yb	10-1	11.8-27.1	1.01-2.21	1.55-9.42	0.41-2.47	0.14-0.39
Lu	10-1	2.51-17.6	-	-	-	-
Hf	1	2.29-4.51	0.16-0.48	0.44-2.06	0.09-0.43	0.002-0.0
Ta	10-1	4.19-6.05	-	-	-	-
Au	10-3	2.40-12.0	4.13-9.44	3.2-19.4	1.40-6.73	5.70-45.9
Hg	10-1	1.92-2.91	1.12-2.25	0.46-5.18	1.35-8.40	1.27-3.07
Th	1	4.13-10.1	0.44-1.01	1.18-5.0	0.23-0.72	0.02-0.03
U	1	1.71-2.29	-	-	-	-

These data were used for the calculation of enrichment factors which can better show the real role of plants in matter accumulation compared to actual concentrations since the latter lacks comparable data.

Enrichment factors for soils, mosses, lichens, tree bark and living leaves are compared in table 2.

In table 2, figures in each column indicate upper and lower levels of the enrichment factors in this order horizontally : soils, lichens, mosses, tree bark and leaves for each element.

In most cases, the enrichment factors for plant material are more than 1.0. The highest factors were found for Cd, Hg, Se, Au.

The soils having the highest estimated actual con-

centrations for most of investigated elements do not have the highest enrichment factors.

Comparing the enrichment factors for soils and lichens, it is seen that, on average, lichens have higher K E than soils and even mosses. For the iron-group elements, KE in lichens are several times higher than those for soils; for Ni, Zn, As, Se, Br, Cd, Cd, Sb, Au, and Hg, these factors are higher by one or more levels of magnitude.

The actual concentration of elements in epiphytic lichens and mosses are, as a rule, lower than in soil-like material under the lichens and mosses on tree trunks. Meanwhile, enrichment factors for the plants are higher from several times to several levels of magnitude. Higher concentrations of elements in the material under the

epiphytes is probably connected with trunk downflow and with the filtering effect of the epiphytic cover. Only for the Se, Cd, Hf, Yb, are the enrichment factors higher for soil than for mosses, and for Mo and Cs higher than for lichens. For some of the elements, the enrichment factors are close -- Na, Cs, La, Eu, Ce, Sm for mosses and soils, and Na, Eu, Yb, Hf for lichens and soils under the epiphytic cover.

It is interesting that the accumulation of elements by mosses near the mud volcanos is very similar to that in industrially polluted areas; elemental concentrations and enrichment factors for Cd, Hg, Mo, Ag are considerably high.

In most samples analysed, tree bark has lower enrichment factors than other plant material. The living leaves of *Quercus robur* had highest factors for K and Au, and considerably high factors for Hg, Cd, Ag, Mo, Br, Se, Cu, and Ca.

Different accumulation in lichens, mosses, soils, tree bark and living leaves show that this process is not only physical. Selectivity of accumulation of different elements is well known for lichens and mosses and often used in background and historical monitoring.

In the situation where pollution source is "natural," we dealt with geochemical anomaly, and it is shown for first time, that most of the elements transported from mud volcano and accumulation by plants is connected with aerosols fine fraction.

This positive experience of element transport estimation using plants confirms the possibility of using lichens and mosses as indicators of natural element flow and background forming monitors.

A National Program for Environmental Monitoring and Assessment

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Background

Increasingly, reports appear on symptoms of current or potential ecosystem problems: declining fish and shellfish harvests and toxic algal blooms in near-coastal waters, dying high-elevation forests, diseased and cancerous fish in lakes and rivers, and declining biodiversity. Because we presently lack an integrated approach to monitoring quantitative indicators of ecological conditions and exposure to pollutants in these ecosystems, we cannot determine whether the frequency, severity, and extent of the problems are increasing on a regional scale, whether such patterns are warning indicators of significant long-term changes in ecosystem structure or function, or whether they are associated with changes in ambient pollutant levels. Lacking a framework for efficiently using data collected by EPA and other organizations or a monitoring scheme to fill the critical gaps in existing data, an assessment of the current status of most environmental problems can be expected to take 4 to 5 years to produce useful results.

EPA, the U.S. Congress, and private organizations with environmental and natural re-

source interests have long recognized a profound need to fill this important monitoring data gap. The need to establish baseline conditions against which future changes can be documented with confidence has grown more acute with the increasing complexity, scale, and social importance of environmental issues such as acid deposition, global atmospheric change, declining biodiversity, and the potential impacts of genetically engineered organisms.

The need for better environmental monitoring systems is not restricted to emerging problems. EPA's Office of Research and Development provides the scientific underpinnings for regulatory programs estimated to cost \$70 billion annually, primarily using laboratory toxicological tests and computer models to predict pollutant transport, fate, and exposure in the environment and their corresponding effects on biota. Years of peer review and litigation have left little doubt that this approach is the only rational way to form the scientific basis for the regulation of the large number of conventional and potentially toxic pollutants that can enter the environment. The potential for differential toxicity to sensitive species, different life stages of the same species, ecological compensation

and magnification, and cascading effects on ecosystem trophic structure, however, all point to the need for validation of the effectiveness of the scientific models through ongoing surveillance of indicators of continuing ecosystem "health."

The problem is not that we have no monitoring data on the environment. Approximately \$350 million is spent each year by EPA on environmental monitoring, about half of which is associated with ambient (as opposed to "source" or compliance) monitoring. This amount is probably at least equaled by other Federal, state, and private organizations. There also have been programs to summarize these data. The EPA Office of Water publishes a biannual status report summarizing the water quality data collected by the states to satisfy section 305(b) of the Clean Water Act; the EPA Office of Air Quality Planning and Standards publishes annual reports on its air quality monitoring program in nonattainment areas; and the President's Council on Environmental Quality and the private Conservation Foundation have summarized monitoring statistics ranging from population levels to the number of Environmental Impact Statements reviewed each year by EPA.

These environmental monitoring programs and interpretive summaries are an important contribution to our knowledge of environmental trends. Lack of comparability of many of the data between programs, together with the absence of a concerted effort to integrate data across networks, however, have thus far prevented these efforts from meeting some of the Agency's critical environmental risk assessment needs. What is currently lacking is a systematic program for assimilating and critically assessing the data with respect to its quality, relevance, comparability, completeness, and above all, for filling critical data gaps.

If such a program were easy or inexpensive to implement, it would certainly already be

in place, and more than one previous effort to design and implement an integrated environmental trends monitoring program within EPA has failed. Many of the obstacles that have frustrated the achievement of this goal in the past, however, may be gone. Successful integrated monitoring and research programs in the Acid Deposition Effects Program, increasing capabilities and opportunities for cooperating with state and other Federal agencies resulting from National Acid Precipitation Assessment Program, the Global Climate Program, the International Geosphere and Biosphere Program of the International Council of Scientific Unions, and a resolve on the part of the Administrator of EPA to increase the emphasis in the Agency on protection of natural ecosystems as well as human health, all pave the road toward potential success.

An Integrated Environmental Research Strategy

In September, 1987, at the initiative of EPA Administrator Lee Thomas, the U.S. Environmental Protection Agency's Office of Research and Development (ORD) directed its scientists to develop an integrated strategy to improve the Agency's ability to assess the risks to natural ecological systems at the regional scale from current and emerging environmental pollutants. Three primary elements were needed to develop this strategy:

- An ecological status and trends program that serves to characterize, classify, and quantify trends in the status of ecological resources and pollutant exposure;
- A core ecological research program to develop tools to predict ecosystem-level responses to incremental changes in anthropogenic activities
- An ecological risk assessment program that allows monitoring and research outputs to be integrated into quantitative esti-

mates of ecosystem-level risks from regulatory policy alternatives.

The Office of Research and Development developed a coordinated strategy for these three elements that utilizes a tiered approach similar to that used in risk assessments for single pollutants. This approach recognizes that, because EPA has insufficient monitoring and research resources to address all ecological problems, it must have an objective basis for identifying the highest priority issues of concern and their current or potential severity on a regional basis. The strategy also recognizes the need to utilize, as fully as possible, current monitoring programs conducted by EPA and other Federal and non-Federal agencies and organizations, working cooperatively to fill any critical data gaps.

In the proposed tiered approach, available biological and chemical monitoring data will be used wherever possible to identify problems and corresponding geographic areas that appear to be at the highest risk. High priority systems will serve as the focus for intensive evaluation of baseline conditions and trend monitoring in the higher tiers, and for research leading to the development of predictive models. Lower priority systems will be subjected to less intensive, surveillance-level monitoring. Monitoring programs will be developed or supplemented to fill data gaps which prevent minimally acceptable surveillance.

An Ecological Status and Trends Program

The first proposed step in the development of the integrated ecological research strategy is creation of the Environmental Monitoring and Assessment Program (EMAP). This program has been proposed by the EPA to begin in FY 1990 to complement its Acid Deposition, Global Climate Effects, and Stratospheric Modification Research Programs. The goal of the Environmental Monitoring and Assessment

Program (EMAP) is to:

Identify, collect, organize, and analyze environmental monitoring data and report periodically to the Administrator on the current status and trends in indicators of the condition of the nation's ecosystems.

Combined with the expertise of the appropriate laboratory, program, and policy office staffs, these data reports and interpretive summaries will enhance the Agency's ability to identify and evaluate emerging environmental issues, to focus scientific assessment programs for high-priority issues on the regions and ecosystems of highest potential concern, and to periodically evaluate the validity of the scientific models upon which risk management strategies are based.

In order to accomplish the program goals, EMAP will be designed to meet the following objectives:

1. Make maximum use of existing monitoring programs to meet EPA's ecological assessment needs and design a program to efficiently fill the critical data gaps
2. Establish baseline conditions and monitor trends in pollutant exposure levels and vital indicators of ecosystem condition for forest, wetland, near-coastal, inland surface water, and agricultural ecosystems on a regional scale
3. Seek and identify relationships between indicators of ecological condition and pollutant exposure that should be considered for in-depth risk assessments by EPA program offices, or that could serve as the basis for important testable research hypotheses or empirical management models
4. Provide a flexible and cost-effective mechanism for responding in a timely way to the

need to assess status and extent of rapidly emerging issues of public concern.

Pollutant "exposure," as used here, may include ambient levels of toxicants, nutrients, microorganisms, or geophysically active substances present in air, wet and dry deposition, surface and groundwater, soil, or biological tissues as a result of human activities, that can result in unanticipated effects on ecosystems. Ecological indicators may include direct or surrogate measures of current or future levels of socially valued ecosystem products, structural or functional ecosystem characteristics, including sustainability, or impacts on adjacent ecosystems.

Approach

The Environmental Monitoring and Assessment Program is planned to be implemented in three phases:

Phase I (present-July 1989): Preparation and Review of Phase II Research Plan

Phase II (August 1989-August 1991): Assessment and Design

Phase III (September 1989-continuing): Phased implementation, beginning with Pilot testing in 1992

The primary outputs of EMAP would be annual environmental statistical reports that describe the regional status of the various indicators and indices chosen for inclusion, and statistical analyses of regional changes and trends. Such results are expected to come from a combination of periodic regional surveys (remeasurements) and more intensive data time-series from selected regionally representative research sites. More extensive interpretive assessments are expected to be produced at 3-4 year intervals.

A number of the tasks that are currently

planned for development in the Phase II Research Plan are summarized briefly below. Although the tasks are listed in approximately sequential order, many can be developed in parallel.

- I. Develop a data management system that catalogs appropriate monitoring programs and their associated data bases and insures efficient access to quality-assured data in a convenient and compatible format
- II. Classify ecosystems into categories that could be monitored using similar measurement techniques and that would respond similarly to pollutant-related stresses
- III. Conduct a screening-level evaluation using available data and studies to identify high-risk or already damaged ecosystem categories and to identify critical data gaps
- IV. Develop, evaluate, and standardize measurement protocols for indicators that best quantify the vital structural and functional aspects of ecosystem condition
- V. Evaluate the applicability of current monitoring network designs, measurement methods, and quality-assurance programs to emerging environmental issues
- VI. Design and assist in the implementation of cost-effective monitoring programs that fill critical data gaps
- VII. Design the annual data reports and summary statistics

Summary and Conclusions

The U.S. Environment Protection Agency is developing research plans for a program to monitor the status and trends in extent, pollutant exposure, and indicators of the condition of ecosystems in the United States. The Phase II Research Plan, which is being readied for peer

review in mid-1989, will describe the research needed to determine whether a program meeting the design objectives of EMAP can begin phased implementation on a pilot basis in 1992,

and, if so, to propose a cost-effective design. If implemented, the program will begin producing annual environmental statistics on an annual basis by 1994.

Biological Diversity and Global Change: Habit Fragmentation and Extinction

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Abstract

Loss of habitat through fragmentation, air pollution, and rapid global climate change forces an international view of the protection of biological diversity. Anthropogenic stresses such as acid deposition, natural resource exploitation, urban sprawl and global warming will undoubtedly cause increased extinction rates. Developing both a common terminology and a conceptual framework for addressing these issues is an important first step to problem solving. We present definitions of key terms and propose the use of habitat fragmentation theory as a "common concern" approach to discuss and understand potential changes in regional and global biological diversity. We urge increased cooperation between the U.S. and U.S.S.R. for additional exchange of cooperative development of inventory and monitoring technologies, joint training of scientists of other nations, and increased environmental education for our citizens and those of other countries.

Introduction

The threat of rapid deterioration of environmental quality and global climate change are crises we face together as common mem-

bers of the biosphere. Tied together by this, we need to accelerate our pace of technological discovery for conservation.

As research on global impacts, such as that of air pollution has shown, the more we threaten our biosphere, the more we ourselves are threatened. We may be among the first, rather than the last, to disappear. Thus, the status of global biological diversity indirectly represents our own capability to endure and survive change.

The subject of maintaining the self-sustaining systems collectively called "biological diversity" (or Biodiversity) is both challenging and complex, and stretches beyond air quality and air pollution. The discovery, observation and protection of biological diversity covers as many different facets as there are disciplines in science and professions in culture and politics. Also included is the broad study of anthropogenic extinction (damage by humans) represented by overconsumption of natural resources, overproduction of waste, overpopulation and fragmented disappearance of natural habitat.

Our research group's specialty is the study of how fragmentation of ecological systems ac-

centuates problems such as pollution and erodes the capability of ecosystems to rebound from progressive catastrophic deterioration. The study of how fragmentation, lack of protection (or ineffective protection) and loss of diversity affect our natural habitats is of common interest to the U.S. and U.S.S.R. How air pollution aggravates fragmentation is something we can monitor and need to cooperate to develop mutually beneficial technologies. To progress in this field, we depend upon common vocabularies in conservation biology that can assist us in communicating what we observe and conceptualize about habitat fragmentation and direct or indirect losses of biodiversity.

Biological Diversity: A Bridge For Communication

Biological diversity, as we conceptualize it, is used to signify the sum of diversity including genetic diversity within and between species, between communities and between higher taxonomic levels (family, ..., class, phylum, kingdom). Biological diversity is not necessarily equal to species diversity, and some groups may house more biological (including genetic) diversity than others. Biological diversity is what generates and results from the ecological and evolutionary processes we observe. The genetic diversity included in biological diversity signifies diversity within the individual among genes that produces phenotypes (or outward manifestations of the individual), diversity between individuals of a gene pool, and diversity between gene pools. Thus, we use genetic diversity to signify the inherited (structural) diversity at, or below, the species level.

Also important are phenotypic diversities, such as behavioral, physiological, etc. We use the term "gene pool" to signify a group or aggregation of interbreeding individuals (not usually a reflection of total diversity within a species), and within each gene pool, there is a certain amount of genetic diversity. For each gene pool, the nature and amount of genetic diversity character-

izes the pool. The gene pool (a genetic term) is also used frequently in *ex situ* conservation in the zoo and botanical garden community when referring to the captive groups of a species. In *ex situ* conservation, scientists and managers more frequently use the demographic term, population, to denote a group of interbreeding individuals. So this demographic term, "population" refers to the organisms, collectively, inhabiting an area or region, as the frog population of a pond. For our purposes, the terms "gene pool" and "population" (of a given species) are synonymous. Once we have described the genetic and demographic components of genetic diversity, we know how it is composed and what constitutes its stability (or instability), both evolutionarily and demographically.

It is the species and population that are generally the focus of environmental research because these comprise the environmental indicators and failing economic resources upon which research focuses. However, communities comprise the group of populations that are ecologically and geographically interconnected, representing a few to several species. Such a group constitutes an assemblage of plants and animals living in a common home, under similar environmental conditions, or with some apparent association of needs. Therefore, the term "community" is meant to suggest more than an environmental indicator or forest resource. It includes the soil microorganisms and all that the landscape can contain within it.

In our inventory and monitoring, we tend to overlook this fact and concentrate too narrowly on a few indicator species we presently consider important. If we take on the responsibility to conserve biological diversity, we are made to view the value of both total protection and multiple resources use, thinking less on the single species as we do the diversity and stability of assemblages of populations. Fortunately, a first measure of their survival is indicated or gauged very effectively by looking at fragmentation of landscapes. Simultaneously identify-

ing and monitoring the conditions of such fragments, we attempt to manage the habitat to reduce unwanted human effects.

Management, whether for parks or other lands, is in danger of being arbitrary and depends upon a policy to guide it. Having a proper guidance policy, management becomes the supportive human involvement in the protection of biological diversity. Management can either be passive (non-interfacing) or active (manipulative or interventionist). The distinction is vague. Management implies the manner of treating a resource for a purpose. This can range from aesthetic purposes to the desire to control a resource. It is the management of fragments in its most simple form that equals park management. Park management includes a full range of characteristics in management. However, opportunities for obtaining large parks (as opposed to fragments) are becoming less common and organizations such as the U.S. National Park Service and our state park systems must increasingly settle for some form of compromise protection, management of damaged systems, and increasingly small reclusive fragments that lack inter-connections. Aside from pollen or seeds that drift with the wind, and a few lucky migratory animals, species diversity declines in stability and quality with the disintegration of landscapes.

Why Does Habitat Fragmentation Threaten Biological Diversity?

In most cases, biological conservation involves protecting fragmented habitats (Wilcove et al., 1986; Noss, 1987). Complete protection of ecosystems or a full spectrum of habitats is rarely achieved. Most reserves are internally fragmented by roads and inappropriate boundaries, a lack of buffer zones and/or a lack of corridors (Wilcove et al., 1986; Noss, 1987; Simberloff and Cox, 1987; Schonewald-Cox and Buechner, in press).

Recently, attention has focused on the

complex nature of size, juxtaposition and properties of administrative boundaries in reserve design and preservation (Schonewald-Cox, 1988; Goodman, 1987a, 1987b; Diamond et al., 1987). Habitat fragmentation can reduce biological diversity in many ways, the most obvious of which is reduced area. Reduction in area may cause a decrease in overall habitat heterogeneity and reduce the role of natural disturbance, and even though on a small scale, increased edge may temporarily increase species diversity. "Generated edges" (SCS, 1987) created by fragmentation adjacent to and within reserves benefit alien/pest species at the expense of endemic species (see also Vitousek et al., 1987). Urban sprawl and resource exploitation adjacent to many nature reserves throughout the world provide a common concern. Likewise, within nature preserves, accommodating visitors and providing for their safety has restricted the role of many natural processes (e.g. lightning-caused fires have been suppressed, insect outbreaks have been controlled, etc.). Once combined, these actions can reduce the biological diversity inside and outside nature reserves.

Wilcove et al. (1986) suggest that habitat fragmentation has two components, both of which cause extinctions: (1) reduction in total habitat area (which primarily affects population sizes and thus extinction rates); and (2) redistribution of the remaining area into disjunct fragments (which primarily affects dispersal and thus immigration rates). We would also add a third component to habitat fragmentation that causes extinction: the process itself is self-driven. Fragments are increasingly likely to be fragmented further as they increase in number or decrease in size.

Potential Impacts of Habitat Fragmentation

The impacts of anthropogenic stresses on natural ecosystems largely depend on the abilities of natural communities to adapt, the rate/in-

tensity/magnitude of the stress, the size of species ranges, the dispersal rates of the individual species, and whether or not barriers to species migration are present (EPA, 1988).

One example is the spotted owl in the U.S. Pacific northwest. Because of its dependence on old-growth Douglas-fir forest which is being harvested, the spotted owl population has declined as edge and open habitat have increased (Harris, 1986).

Most breeding pairs of spotted owls require a fixed amount of old-growth forest. Long-term population survival will probably depend on maximum limits for immigration distances of the owls. If the species is to survive, remnant patches will need to be separated by distances (between "islands") of old-growth forests that do not exceed natural juvenile dispersal movement. Harris stresses the importance of planning and understanding the spatial patterns of forest fragments. In light of world-wide increases of anthropogenic stress on natural ecosystems, Harris' conceptual model can and must be applied on a global scale.

Superimposed on fragmentation are effects of air pollution on forests, soils and water which have long been documented with the most powerful example of large scale die-offs we have seen previously from Germany (Proceedings of this Symposium, Smith, 1981; Reuss and Johnson, 1986; Blank, 1985). But, in many cases, including our own most protected National Parks, subtle ecosystem changes may be taking place because of changes in wet deposition chemistry (Stohlgren and Parsons, 1987) or ozone concentrations (Bennett, 1985). Individual species response (e.g. pine species may be pre-disposed to insect diseases) or inter-specific dynamics (i.e. favoring air pollution-tolerant species) are difficult to monitor and assess.

Climatic change, also of interest to these proceedings, will alter competitive outcomes

and destabilize natural systems in unpredictable ways (EPA, 1988). It is unknown to what extent climate change will cause changes in species composition, food availability, predator/prey relationships or many other ecosystem components. It is known that species ranges will change (EPA, 1988; Peters and Darling, 1985), and fragments will not move with them.

Peters and Darling (1985) provide a diagrammatic model of how climate change or shifting pollution (acid rain) might influence the species composition of a biological reserve. Similarly, in our studies of National Parks we are faced with planning probable scenarios. For example, imagine a reserve in which Species A is pushed northward by global warming into habitat of mixed suitability (Figure 1). Species A may survive in pockets of this habitat as environment pushes its dispersers further north. Perhaps a new reserve can be established in its new habitat while the old reserve becomes home to new species assemblages. Unfortunately, such a late establishment of the new reserve is likely to be accompanied by severe compromises and keep species A and cohorts in less than optimal conditions. In a worst case scenario, development and extensive habitat fragmentation have removed even the opportunities for the establishment of species A in "mixed-suitability" sites. Species A becomes locally extinct as its southern limit moves north and meets the progressive development.

Boundaries of the park are fixed. Species A and its associates will be eventually replaced in the reserve. If the new species dispersing and filling the reserve are non-desirable, such as alien plants or animals, ecosystem processes will also be transformed. Should a replacement species be a woody species, more flammable than Species A, for example, it would promote increased intensity and frequency of wildfires. In our current times in which the spread of alien species has threatened representative ecosystems, such changes could exacerbate initial impacts (Vitousek et al., 1987a and b). Such

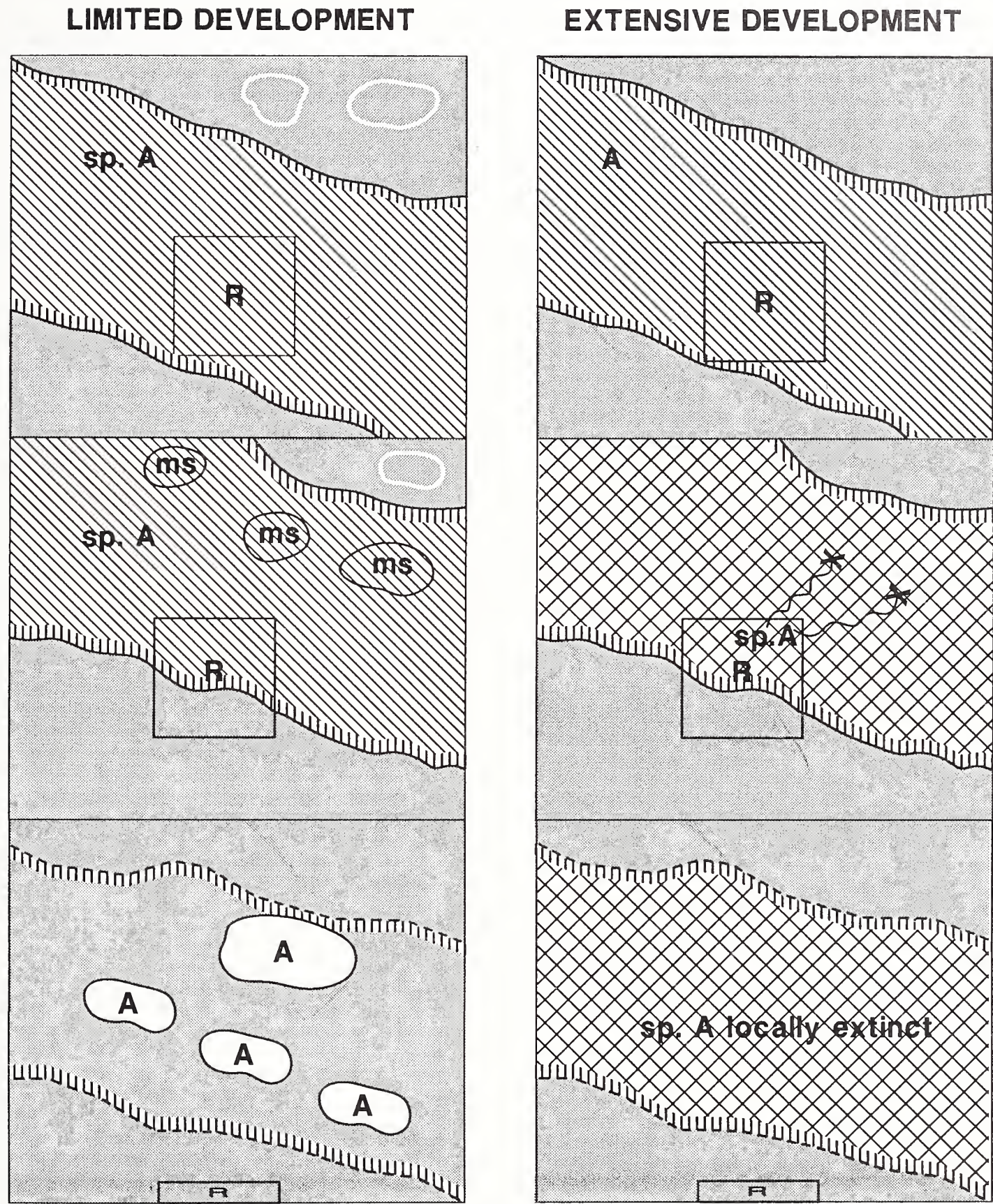


Figure 1. Extinction, environmental change and development. In the figure on the left, a reserve (R) exists in the deteriorating range of species A (hatched area). Fatal sinks exist (solid black) beyond the tolerance limits of species A (□□ : to the north; and □□ : to the south). As environmental changes move north, species A dispersers find refuges of mixed suitability (ms). Soon these are the only remaining sites where A can be found. In another scenario (figures on the right), extensive human development is expanding to the north. As environmental changes move northwardly, they overlay human development (grid), and dispersers of species A have no "ms" habitat available. Extinction follows for lack of habitat.

changes are bound to decrease the local variety of native species, perhaps increase overall species diversity, but decrease biological diversity at the continental level.

Given paleo-ecological migration rates of some forest species (e.g. 10-20 km per century for chestnut, maple and balsam fir, and between 30-40 km per century for some oak and pine species; EPA, 1988), small reserves may be affected more quickly than large reserves in the same area. As was suggested by Wilcove et al. (1986) and ourselves in the previous section, small fragments are more likely to be depleted than large landscape fragments.

Uncertainties Associated With Change

Strategies for slowing deleterious effects of habitat fragmentation, and associated losses in biological diversity will be difficult to come by. Conservation Biology and Landscape Ecology (including study of fragmentation) are still very young disciplines. We currently possess only a crude understanding of the links between our respective societies and the environment and climate (EPA, 1988). Taken in reverse order, the uncertainties of climate change (it's actual rate and potential effects) are enormous. Models used to predict climate change are in their infancy and are propelled by poor and incomplete data. Often, competing models give conflicting results (EPA, 1988). Little is known about sensitivity, direction and magnitude, and linkages of climatic variables. Given our current knowledge, it is difficult or impossible to predict regional changes.

Our current understanding of environmental variables is only slightly ahead of the case above. The widely-accepted paradigm is that local climate is the primary factor defining the environmental setting and determines the species composition and spatial patterns of communities in terrestrial zones (Bolin et al., 1986). We would add the complex contributions of inter- and intra-specific competition,

predation, insects and disease and local disturbance frequency and intensity, and the interactions of these with species population dynamics. Still, this model may be replaced by an infinitely more complex model incorporating climate change, depletion of stratospheric ozone, the presence of tropospheric ozone and acid deposition, and changes to the disturbance regimes brought about by climate change (EPA, 1988).

At the present time, we are also unable to predict the details of how fragmentation and anthropogenic stresses will affect species extinctions. We have few, if any cases, where the autecological information base on a species is complete enough to predict extinction under different environmental scenarios. Likewise, extinction models (MacArthur and Wilson, 1967; Quinn and Hastings, 1987; or see Burgman et al., 1988 for a review) have not been designed to address species-specific changes to environmental conditions.

The linkage between our societies to the environment and climate is also poorly understood. How quickly can world economies and resource use patterns be altered to reduce the impacts of anthropogenic stresses on biological diversity? Are we willing to make those changes?

Perhaps it is this most damaging issue that we need to address further together. How will air pollution, global climate change and habitat loss affect the ability of species to disperse? Also, where can they disperse to now and 20 years from now given the current rate of fragmentation? And, which of these will be among the projected percentage of extinctions? This dispersal is fundamental to the maintenance of species and the generation of new ones. Because environmental change is certain, changes in natural selection are also certain. Few, if any, species will remain tomorrow as they are today. The few that are unresponsive to selection will disappear. We need to cooperate on the study of these broader topics in conservation. We

certainly can find commonality in the descriptions of biodiversity (and methods of fragmentation), fragmentation of landscapes and effects of environmental change on those habitats still available in nature.

Maintaining Biological Diversity

Given the above uncertainties, perhaps our efforts to conserve species would best be focused on maintaining the current biological diversity, increasing our understanding of fragmented landscapes and anthropogenic stresses, and increasing cooperation between the U.S. and U.S.S.R. as leaders in the efforts for long-term global habitability. The U.S. and U.S.S.R. have the greatest opportunity to provide world leadership in the protection of biological diversity in fragmented landscapes. Active leadership in the United Nations Environment Program (UNEP), the World Meteorological Organization (WMO) and the International Panel on Climate Change (IPCC) is an important first step. We must build on the success of the Man and the Biosphere (MAB) program and the Montreal Protocol to protect the Ozone Layer. The U.S. National Park Service stated what it viewed as specific needs with respect to cooperation in managing for viable populations in changing landscapes. Emphasizing multi-agency and multinational cooperation, these needs are probably similar in both the U.S. and the U.S.S.R. They are:

1. The management of viable populations of target species.
2. The preservation of variation within species in communities extending beyond National Park boundaries and regional landscapes.
3. Attention to external breaks in distributions and resultant losses of migratory species to the effects of tropical deforestation, pollution, or climate change.
4. Cooperation in the development and translation of technologies and exchanges of information on inventory, monitoring, long- and short-term research, interpretation, education, and

funding of protection for biological diversity.

These needs are not limited to parks and reserves but are required on large geographic scales that incorporate the full diversity of existing habitats, both small and large, from hedge rows, ponds, to riparian and oceanic habitats.

Increased Cooperation in U.S.-U.S.S.R. Efforts

Bilaterally, the U.S. and U.S.S.R. can serve as the international model in the protection of biological diversity through more frequent interactions between scientists and increased exchanges of data, scientific publications, techniques and dialogue. We can jointly develop baseline inventory and monitoring techniques and associated research, education and training activities with less-developed countries. Perhaps and most importantly, we can educate our citizens with regional and global perspectives in ecology and environmental awareness. We can actively disseminate information on biological diversity through international interpretive programs. We should stress the interdependence of our protected areas and the necessary linkages between socio-political systems required to protect these areas.

Literature Cited

- Bennett, J.P. 1985. *Known air pollution effects on vegetation in National Parks*. Testimony presented to the House Subcommittee on National Parks and Recreation, Committee on Interior and Insular Affairs, U.S. Congress, May 1985.
- Blank, L.W. 1985. A new type of forest decline in Germany. *Nature* 314:311-314.
- Bolin, B., B. Doos, J. Jager, and R. Warrick (eds.). 1986. *The Greenhouse Effect, Climate Change and Ecosystems* (Scope 29). John Wiley and Sons, Chichester.
- Burgman, M.A., H.R. Akcakaya, and S.S. Loew. 1988. The use of extinction models for species conservation. *Biological Conservation* 43:9-25.

- Diamond, J.M., K.D. Bishop, and S. vanBalen. 1987. Bird survival in an isolated Javan woodland: island or mirror. *Conserv. Biol.* 1:132-142.
- Environmental Protection Agency. 1988. *The potential effects of global climate change on the United States*. Draft Report to Congress. U.S. EPA, Washington, D.C.
- Goodman, D. 1987a. Considerations of stochastic demography in the design and management of biological reserves. *Natural Res. Modeling* 1:205-234.
- Goodman, D. 1987b. How do any species persist? *Lessons for conservation biology* 1:59-62.
- Harris, L.D. 1986. *The fragmented forest: Island biogeography theory and the preservation of biological diversity*. University of Chicago Press, Chicago, IL.
- MacArthur, R.H., and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Myers, N. 1987. Not Far Afield: U.S. Interests and the Global Environment. *World Resources Institute Report No. 5786*. Washington, D.C.
- Noss, R.F. 1987. Protecting natural areas in fragmented landscapes. *Natural Areas Journal* 7(1):2-13.
- Quinn, J.F., and A. Hastings. 1987. Extinction in subdivided habitats. *Conservation Biology* 1(3):198-208.
- Peters, R., and J. Darling. 1985. The greenhouse effect and nature reserves. *Bioscience* 35(11):707-717.
- Reuss, J.O., and D.W. Johnson. 1986. *Acid Deposition and the Acidification of Soils and Waters*. Springer-Verlag, New York, N.Y.
- Salwasser, H., C.M. Schonewald-Cox, and R.J. Baker. 1987. The role of interagency cooperation in managing for viable populations. In: M.E. Soule (ed.) *Viable Populations*. Cambridge Univ. Press, Cambridge, U.K.
- Schonewald-Cox, C.M. 1988. Boundaries in the protection of nature reserves; translating multi-disciplinary knowledge into practical conservation. *Bioscience* (in press).
- Schonewald-Cox, C. M. and M. Buechner. 1989. Fragmentation of ecosystems and America's crown jewels. In: P.L. Fiedler and S. Jain (eds.) *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management*. Chapman and Hall, NY. (in press)
- Schonewald-Cox, C.M., S.M. Chambers, B. MacBryde and L. Thomas (eds.). 1983. *Genetics and conservation*. Benjamin Cumming, Menlo Park, CA.
- Simberloff, D.S., and J. Cox. 1987. Consequences and costs of conservation corridors. *Cons. Biol.* 1:63-71.
- Smith, W.H. 1981. *Air Pollution and Forests*. Springer Verlag, New York, N.Y.
- Stohlgren, T.J., and D.J. Parsons. 1987. Variation of wet deposition chemistry in Sequoia National Park, California. *Atmospheric Environment* 21:1369-1374.
- Vitousek, P.M., L.L. Loope, and C.P. Stone. 1987. Introduced species in Hawaii: biological effects and opportunities for ecological research. *Trends in Ecology and Evolution* 2(7):23-37.
- Vitousek, P.M., L.R. Walker, L.D. Whiteaker, D. Mueller-Dombois, and P.A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802-804.
- Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. P. 237-256. In: M.E. Soule (ed.) *Conservation Biology*, Sinauer, Sunderland, MA.

Relations Between Forest Conditions and Atmospheric Deposition Along the Northwestern Minnesota-to-Southeastern Michigan Deposition Gradient

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Abstract

A distinct gradient of emission-related sulfate deposition increases from near background levels in northwestern Minnesota to moderately high levels in southeastern Michigan. Wet sulfate deposition patterns along this gradient are shown to be reflected in soils of forest ecosystems, and a terrestrial sulfur gradient from northeastern Minnesota to southeastern Michigan is correlated with the sulfate deposition gradient in precipitation. The strongest relations between diameter growth and estimated sulfate deposition on the 171 study plots were for jack pine, red pine (negative relation between sulfate deposition and growth), and sugar maple (positive relation). Although statistically significant, relations are weak and obscured by large natural variation in diameter growth rates. The effects of deposition are confounded with effects of climate due to high correlations between the deposition levels along the gradient and certain climatic variables. The data examined thus far make it impossible to conclude that sulfate is a major factor affecting tree growth in the Lake States. With the techniques used in this study, up to one-half of the total variation in tree diameter growth could be explained. Of the

part that could be explained, one-fifth to one-third was associated with climatic variation, sulfate deposition, other unknown factors highly correlated with sulfate deposition or climate, or some combination of the above.

Introduction

Atmospheric pollutants may be affecting the health of the nation's forests. Scientists have observed foliar damage, unexplained decline, and abnormal death of trees of various species in the eastern United States (Barnard, 1986). The possibility that atmospheric pollutants are involved is frequently suggested by members of the scientific community and reported by the media. The total geographic extent and magnitude of possible effects of air pollution on forest trees are unknown (Barnard, 1986). One way to determine the existence or extent of forest damage is through broad surveys of forest conditions that search for patterns in relations between forest conditions and atmospheric deposition or other environmental factors (Barnard, 1986).

We evaluated forest conditions along a gradient of wet sulfate (SO_4) deposition ranging

from near natural background levels in northwestern Minnesota to moderately high pollution-derived levels in southeastern Michigan. Our general hypothesis is that the wet sulfate deposition gradient across the Lake States is reflected in the amount of accumulated sulfur in the forest floor-soil system and tree tissue, and is related to differences in tree radial increment, and that these effects can be separated from those of climate and site conditions. The following subsidiary hypotheses are addressed in this paper: (1) sulfur concentrations in the forest floor and mineral soil do not correlate positively with the sulfate deposition gradient in wet precipitation (National Atmospheric Deposition Program) from northwestern Minnesota to southeastern Michigan, and (2) when adjusted for species, site quality, competition and climate, observed

tree growth is independent of estimated sulfur deposition and concentration of sulfur in the tree woody tissue.

Methods

Due to restrictions on manuscript length, explanation of methodology is abbreviated; full details can be found in Ohmann *et al* (1988).

This study was designed to elucidate relationships, rather than to determine cause and effect. To facilitate sampling selection and testing of the hypotheses, the gradient was divided into 5 zones (Figure 1). The zone boundaries roughly correspond to the 1, 2, 4, and 8 kg ha⁻¹ yr⁻¹ isolines of the acid sulfate deposition gradient (Nichols and Verry, 1985; Verry and

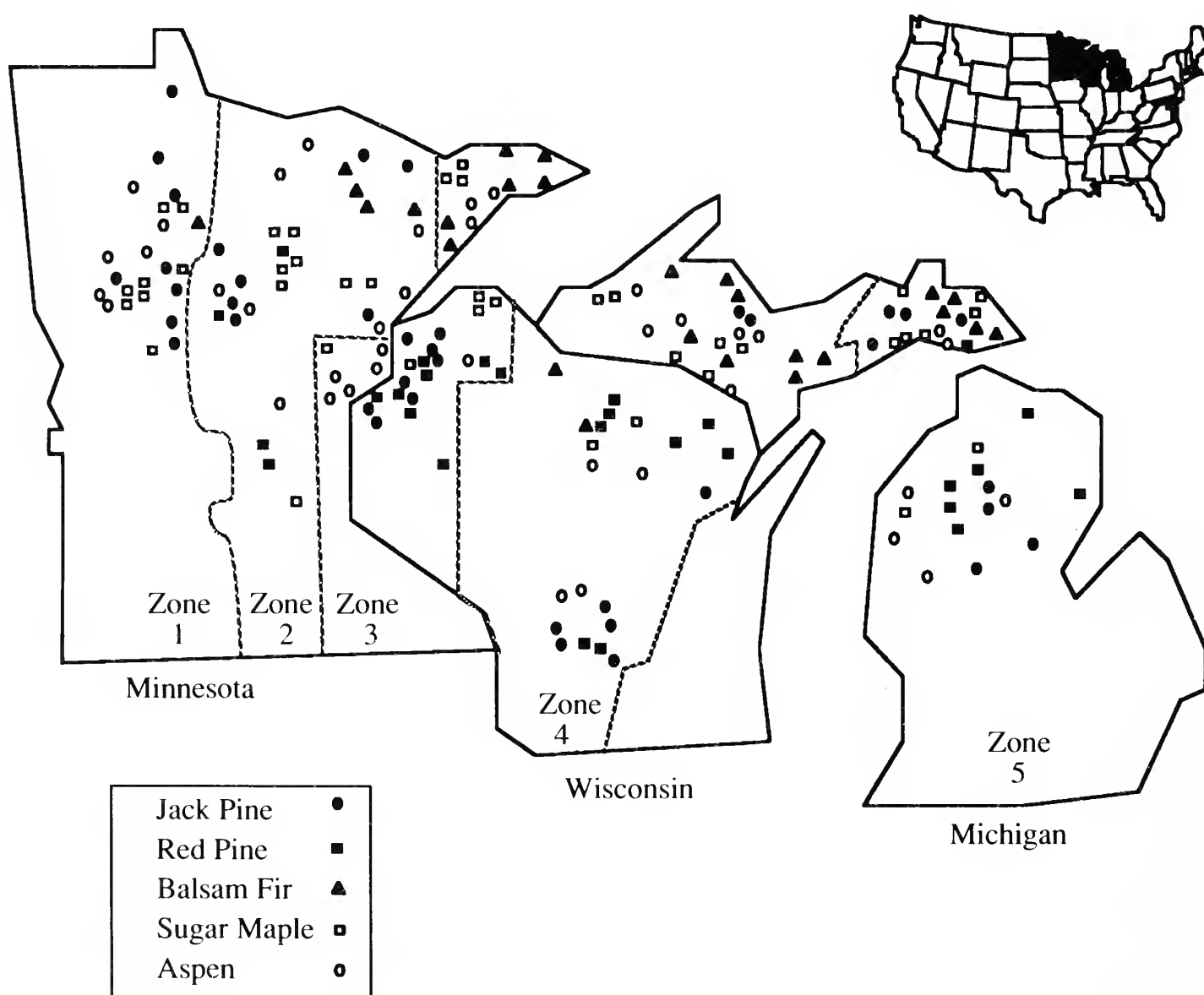


Figure 1. Sample plot distribution by forest type and zone across the sulfate deposition gradient.

Harris, 1988), which is equivalent to the 10, 11, 13, and 17 kg ha⁻¹ yr⁻¹ isolines of the total sulfate deposition gradient.

We focused on two hardwood and three softwood species that occur across the gradient. Three of the species are shade-intolerant: aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), and red pine (*Pinus resinosa*). The other two are shade-tolerant: sugar maple (*Acer saccharum*) and balsam fir (*Abies balsamea*).

The field locations sampled in 1985 were selected from more than 20,000 Forest Inventory and Analysis (FIA) plots that had been permanently established between 1976 and 1982. FIA forest survey plots for the Lake States were screened to identify 171 plots of the five forest types of interest, evenly spread across the five zones and having a limited range of initial densities, ages, and site indices (Figure 1). Numerous measurements were made at each study site, including current tree diameter, crown class, measures of stand density, site index, aspect, and slope.

Samples of the forest floor and mineral soil were collected around five selected trees on 169 plots and returned to the laboratory for chemical analysis. The chemical content of woody tissue samples from those trees was also analyzed.

Plot-specific sulfate levels were estimated from atmospheric monitoring stations, from chemical analyses of the soil, and from chemical analyses of woody tree tissue. Atmospheric sulfate deposition for each sample plot was estimated as the product of annual precipitation and the concentrations of sulfate per unit of precipitation. Plot-specific precipitation values were estimated from 30-year normal values (1951-1980) for 395 weather stations throughout the Lake States. Mean annual precipitation for each plot was computed as the distance weighted average for the four weather stations nearest to each plot. The concentration of sul-

fate in rainfall for each plot was found to be adequately estimated using a model relating latitude and longitude to the mean annual volume-weighted sulfate concentrations in precipitation collected at monitoring sites operated by the National Atmospheric Deposition Program and the Minnesota Pollution Control Agency. Plot-specific deposition was estimated as the product of the precipitation and concentration estimates.

We recognized that sulfate deposition is only one of many factors that can affect tree growth. Thus, we tested whether or not significant relations between diameter increment and sulfate level exist after accounting for variation in tree species, tree size, site quality, tree density, and climate. Individual tree diameter growth rates were predicted using the STEMS (Brand *et al.*, 1988) tree growth projection system, adjusted for climatic patterns, and using an empirical linear model.

Results

Forest Floor--Estimated sulfate deposition for the plots ranged from 156 to 380 eq ha⁻¹ yr⁻¹ in zones 1 through 5 and was significantly different among zones ($P < 0.01$), suggesting that the estimates for the zones reflect the sulfate gradient.

Concentrations of total carbon (C) and nitrogen (N) in the forest floor were similar for zones 1, 2, and 3. Zone 4 had the highest concentration of these elements; zone 5 was lower than 4 but higher than zones 1 through 3. For mineral soils, these elements were not significantly different in concentration across the zones ($P > 0.05$) (David *et al.*, in press).

Total sulfur (S) and N concentrations were highly correlated (R-square of 0.96, $n = 1765$, $P < 0.001$) as would be expected because both are primarily found in organic forms in most soils. Sulfur and N concentrations in soil organic matter are affected by both climatic and vegeta-

tion factors. To eliminate variation in S related to those factors, total S concentrations were adjusted for total N by analysis of covariance among zones. For both forest floor and mineral soils, the adjusted total S concentration stayed relatively constant in zones 1 through 3, and increased significantly ($P < 0.05$) in zones 4 and 5. The increase in zone 5 suggests a 15 percent higher S concentration; atmospheric deposition of S is a potential source for this increase (David *et al.*, in press).

The increase in total S concentrations adjusted for total N in forest floors and mineral soils across the gradient suggests rejecting the null hypothesis related to forest floor and mineral soil sulfur concentrations. The results suggest that sulfate deposition patterns are reflected in forest soil systems, and that there is a terrestrial sulfur gradient across the Lake States related to the previously demonstrated sulfate deposition gradients in precipitation and clear-water lakes (Verry and Harris, 1988; Nichols and McRoberts, 1986).

Diameter Growth --- All analyses testing relationships between tree radial growth and sulfate deposition were based on data from the 171 remeasured forest inventory plots (Figure 1) and have focused on individual tree diameter growth rates. To further simplify interpretation of results, only trees that were between 13 and 23 cm dbh at the first measurement were included in these tests. Also, analyses were limited to a single species within each of the five forest types of interest (e.g., only jack pine trees growing on jack pine plots were analyzed together, only red pine trees growing on red pine plots, etc.). Only trees that were alive at both measurements have been included, resulting in between 142 and 337 observations per species. For purposes of comparison, all periodic diameter growth observations were converted to annual rates.

The null hypothesis, that periodic tree di-

ameter growth is independent of the level of sulfate deposition at the site where those trees are growing, was tested by comparing observed diameter growth rates with two different predictions of diameter growth rate for each tree. In the absence of effects of sulfate deposition, differences between observed and predicted tree diameter growth rates were expected to be uncorrelated with the level of sulfate deposition. The following statistical tests do not make an *a priori* assumption that the relation between sulfate deposition and tree growth is strictly a negative one. However, in the analyses, the sign of the estimated regression coefficients for sulfate deposition indicates whether the level of sulfate deposition appears to be detrimental or beneficial to tree growth.

The general model used to test the hypothesis is:

$$\Delta D_i = f(\text{species, size, competition, crown size, site quality...}) + g(\text{climate}) + e_i \quad [1a]$$

vs

$$\Delta D_i = f(\text{species, size, competition, crown size, site quality...}) + g(\text{climate}) + h(\text{SO}_4) + e_i \quad [1b]$$

where:

D_i = observed periodic annual dbh growth of the i th tree

$f(\text{species, size...})$ = any model predicting dbh growth as a function of biological or edaphic factors other than climate and SO_4

$g(\text{climate})$ = a function of climatic variables expected to affect periodic tree dbh growth

$h(\text{SO}_4)$ = a function of the estimated sulfate deposition or sulfate impact at each plot

e_i = the error term, assumed normally distributed with constant variance and mean zero

SO_4 = estimated SO_4 ($\text{kg ha}^{-1} \text{ yr}^{-1}$) at each site

e_i = error term

Two different tree growth models were used to represent the term $f(\text{species, size, competition, crown size, site quality...})$ in equations [1a] and [1b]. The first was the STEMS/TWIGS tree growth projection model for the Lake States (Brand *et al.*, 1988). The STEMS/TWIGS models are a system of individual-tree, distance-independent models calibrated for species in the North Central United States. STEMS/TWIGS was used to predict diameter growth of the sampled trees, taking into account tree size, crown size, size relative to competitors, density, and site quality. Differences between the predicted and observed periodic diameter growth rates for each species were examined. If SO_4 was having a detrimental effect on tree growth, then the differences between the observed and predicted growth rates should become large and negative as SO_4 deposition increases.

The second model used to represent the term $f(\text{species, size, competition, crown size, site quality...})$ in equations [1a] and [1b] was a linear model of a number of variables observed at the initial measurement of the 171 study plots. These variables included diameter, crown class, crown ratio, stand density, relative tree size, and site characteristics.

The term $g(\text{climate})$ was represented by a linear combination of the variables in Table 1, for conifers and hardwoods, respectively. In a separate analysis, Holdaway (1988 and personal communication 12/87) found these variables to be most strongly related to diameter growth for the three conifer and two hardwood species examined in this study. Weather variables for each plot were averaged over the re-measurement interval from observations recorded at the weather station nearest each plot.

The effect of sulfate deposition was represented by the linear term, $\beta_0 + \beta_n \text{SO}_4$. An F-test (McRoberts, 1988) was used to evaluate the significance of coefficient β_n , which indicated the importance of SO_4 in explaining variation in diameter growth. The corresponding pairs of models are:

$$\Delta \text{Di} - f(\text{STEMS}) = \beta_0 + g(\text{climate}) + e_i \quad [2a]$$

vs

$$\text{Di} - f(\text{STEMS}) = \beta_0 + g(\text{climate}) + \beta_n \text{SO}_4 + e_i \quad [2b]$$

and

$$D_i = \beta_0 + f(\text{species, size, competition, crown size, site quality...}) + g(\text{climate}) + e_i \quad [3a]$$

vs

$$D_i = \beta_0 + f(\text{species, size, competition, crown size, site quality...}) + g(\text{climate}) + \beta_n \text{SO}_4 + e_i \quad [3b]$$

Table 1. Monthly and seasonal climatic variables found by Holdaway^a to have high correlations with patterns of tree diameter growth in the Lake States.

Conifers	Hardwoods
Mean November temperature	Mean December temperature
Total July precipitation	Total June Precipitation
Total March precipitation	Proportion of annual ppt. in Sep., Oct. & Nov.
Proportion of annual ppt. in Dec. & Jan	Proportion of annual ppt. in Dec.
No. days with ppt. > 0.5" in Sep., Oct., & Nov.	No. days with ppt. > 0.5" in Jun., Jul. & Aug.
Temp. x ppt. for Dec. & Jan.	Temp. x ppt. for Nov. & Dec.
Temp./ppt. for July and Aug.	
Ppt./temp. for Oct & Nov.	

^a From Holdaway (1988) as amended by personal communication, Margaret Holdaway (12/87) to emphasize the species of interest in this study.

Table 2. Summary of regression results for models [2a] and [2b] with an F-test for the significance of the sulfate deposition term in describing patterns of tree dbh growth.

Species	Model [2a] without SO ₄				Model [2b] with SO ₄				Fb
	n	R ²	SSE ^a	d.f.	R ²	SSE ^a	d.f.	[^] βn	
Jack pine	305	.11	.793	26	.13	.781	295	-.006	4.5*
Red pine	313	.21	1.543	304	.23	1.508	303	-.009	7.0**
Balsam fir	142	.21	.246	133	.21	.246	132	.001	0
Sugar maple	198	.20	.511	191	.24	.485	190	.011	10.2**
Quaking aspen	205	.07	.771	198	.09	.752	197	.011	5.0*

^a Total error sum of squares

^b F-test comparing models [2a] and [2b]. This F-value indicates the importance of the SO₄ term after all other terms have been included in the model.

Table 3. Summary of regression results for models [3a] and [3b] with an F-test for the significance of the sulfate deposition term in model [3b] in describing patterns of tree dbh growth.

Species	Model [3a] without SO ₄				Model [3b] with SO ₄				Fb
	n	R2	SSE ^a	d.f.	R2	SSE ^a	d.f.	βn	
Jack pine	305	.35	.645	283	.36	.641	282	-.004	1.8
Red pine	313	.48	1.154	291	.49	1.138	290	-.009	4.1*
Balsam fir	142	.44	.176	120	.44	.176	119	-.001	0
Sugar maple	198	.47	.402	178	.51	.377	177	.014	11.7**
Quaking aspen	205	.33	.567	185	.33	.563	184	.006	1.3

^a Total error sum of squares

^b F-test comparing models [3a] and [3b]. This F-value indicates the importance of the SO₄ term after all other terms have been included in the model.

where f(STEMS) is the known estimate of dbh growth from the STEMS/TWIGS model; f(species, size, competition, crown size, site quality...) is the linear combination of terms described above; and g(climate) is the linear combination of terms (for conifers and hardwoods, respectively) identified in Table 1.

The left side of equations [2a] and [2b] are simply the differences between the observed periodic diameter growth and the STEMS/TWIGS prediction of that growth. The null hypothesis of no sulfate deposition effect is rejected for ~3n significantly different from zero. Weather variables were averaged for the weather station nearest each plot.

Shifley (1988) used a series of additional models to examine relations between tree radial growth and estimated SO₄ deposition exclusive of adjustments for differences in competition, stand conditions, and weather.

Results (Table 2) indicate that with the STEMS/TWIGS model as an indicator of expected stand change (equations [2a] and [2b]), periodic tree diameter growth for jack pine, red pine, sugar maple, and aspen was significantly related to estimated sulfate deposition (P<0.05). However, for sugar maple and aspen trees, diameter growth increased with increases in the estimated sulfate deposition.

When effects of sulfate deposition on tree

growth were evaluated in a general linear model of tree dbh growth (with models [3a] and [3b]), the results changed somewhat (Table 3). The only significant relations ($P < 0.05$) between diameter growth and estimated sulfate deposition were observed for red pine and sugar maple. As before, dbh growth for red pine decreased and dbh growth for sugar maple increased with increasing sulfate deposition.

In the best case, these models accounted for only about half of the total variation in tree diameter growth for this data set. Although statistically significant in several cases, the sulfate deposition term accounted for no more than an additional four percent of this variation after all other terms were in the model.

The sulfate deposition gradient is confounded with climatic gradients. Correlations among estimated deposition and climatic variables were generally between 0.5 and 0.9, making it impossible to conclusively distinguish effects due to the SO_4 gradient from effects due to the climatic gradients. In combination the climatic variables and the estimated sulfate deposition accounted for between 6 and 15 percent of the total variation in tree diameter growth, or about one-fifth to one-third of all the variability in diameter growth that was explained by these models. Overall, the strongest relations between diameter growth and sulfate deposition were for jack pine, red pine, and sugar maple.

Literature Cited

- Barnard, J. E. 1986. *National Vegetation Survey Program Plan. Forest Response Program*, U.S. Dept. of Agric., Forest Service, Washington, D.C. 41pp + appendices.
- Brand, G. J., M. R. Holdaway, and S. R. Shifley. 1988. A description of the TWIGS and STEMS individual tree-based growth simulation models and their applications. pp 950-959 In: A. R. Ek, S. R. Shifley, and T. E. Burk (eds.) *Forest growth modelling and prediction: proceedings of the IUFRO conference*. August 23-27, 1987, Minneapolis, MN. General Technical Report NC-120, U.S. Dept. of Agric., Forest Service, North Central Forest Experiment Station, St. Paul, MN, 1150pp.
- David, M. B., D. F. Grigal, L. F. Ohmann, and G. Z. Gertner. In press. S, C, and N relationships in forest soils across the northern Great Lake States as affected by atmospheric deposition and vegetation. *Canadian Journal of Forest Research*.
- Holdaway, M. R. 1988. The relationship between tree diameter growth and climate in the Lake States. pp 490-497 In: A. R. Ek, S. R. Shifley, and T. E. Burk (eds.) *Forest growth modelling and prediction: proceedings of the IUFRO conference*. August 23-27, 1987, Minneapolis, MN. General Technical Report NC-120, U.S. Dept. Agric., Forest Service, North Central Forest Experiment Station, St. Paul, MN, 1150pp.
- McRoberts, R. E. 1988. Comparing regression curves. pp 762-769 In: A. R. Ek, S. R. Shifley, and T. E. Burk (eds.) *Forest growth modelling and prediction: proceedings of the IUFRO conference*. August 23-27, 1987, Minneapolis, MN. General Technical Report NC-120, U.S. Dept. Agric., Forest Service, North Central Forest Experiment Station, St. Paul, MN, 1150p.
- Nichols, D. S. and R. E. McRoberts. 1986. Relations between lake acidification and sulfate deposition in northern Minnesota, Wisconsin, and Michigan. *Water, Air, and Soil Pollution* 31: 197-206.
- Nichols, D. S. and E. S. Verry. 1985. Evidence for the cultural acidification of lakes in the northern Lake States. pp 253-265 In: *Air pollutants effects on forest ecosystems*. May 8-9, 1985. The Acid Rain Foundation, St. Paul, MN.
- Ohmann, L. F., S. R. Shifley, and M. R. Holdaway. 1988. *The relationship between various aspects of forest conditions and atmospheric deposition across the northwestern Minnesota-to-southeastern Michigan deposition gradient*. Unpublished final report submitted to Program Manager, National Vegetation Survey, Forest Response Program, National Atmospheric Precipitation Assessment Program. Available from authors, U.S. Dept. of Agric., Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Shifley, S. R. 1988. Analysis and modelling of forest growth trends along a sulfate deposition gradient in the North Central United States. pp 506-513 In: A. R. Ek, S. R. Shifley, and T. E. Burk (eds.) *Forest growth modelling and prediction: proceedings of the IUFRO conference*. August 23-27, 1987, Minneapolis, MN. General Technical Report NC-120, U.S. Dept. Agric., Forest Service, North Central Forest Experiment Station, St. Paul, MN, 1150pp.

Verry, E. S., and A. R. Harris. 1988. A description of low- and high-acid precipitation. *Water Resources Research* 24(4): 481-492.

CO₂-Induced Climate Change and Forest Resources¹

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Forests both affect and respond to changes in atmospheric CO₂ and climate. Forests directly affect climate at the global scale by altering the earth's albedo, hydrological regimes, and atmospheric CO₂. At a local scale they can alter air temperature, humidity, and solar radiation. In turn, forests are affected by CO₂ and climate at many spatial and temporal scales. The objective of this paper is to examine potential forest responses to increases in atmospheric CO₂ and to CO₂-induced climate change.

Forest responses to CO₂ and climate may be examined by using five biotic paradigms (Table 1). Each paradigm has its own spatial and temporal scale and its own set of unique phenomena responsive to CO₂ and climate change. We will first use these paradigms to review forest responses to CO₂ and climate. We will then describe the linkages between these paradigms and the implications of these linkages for future research on the impact of elevated atmospheric CO₂ and climate change on forest resources.

Biosphere

The biosphere paradigm is concerned with global fluxes of carbon, energy, and water. It is within this paradigm that feedbacks between climate, atmospheric CO₂, and forest resources are most apparent.

Biosphere carbon fluxes are, in part, regulated by global vegetation because carbon, the major constituent of plants, is absorbed from the atmosphere as CO₂ through photosynthesis and is returned to the atmosphere when plants respire or die and decompose. Thus, the accumulation of biomass is a major regulator of atmospheric CO₂. Because current atmospheric CO₂ partial pressures are generally considered suboptimal for photosynthesis, an increase in atmospheric CO₂ should increase net photosynthesis in the absence of any other considerations (Kramer and Sionit, 1987).

Biosphere energy fluxes are both directly and indirectly influenced by global vegetation.

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Table 1. The spatial scale, temporal scale, and key phenomena within biotic paradigms in which forests respond to climate and CO₂

Paradigm	Spatial Scale	Temporal Scale	Phenomena of relevance
Biosphere	Globe	Years-millennia	Energy, carbon, water fluxes
Biome	Subcontinental	Centuries-millennia	Evolution/extinction, migration
Ecosystem	10 ¹ -10 ⁴ ha	Years-centuries	Disturbance, nutrient cycling
Stand	10 ¹ -10 ³ ha	Years-decades	Competition, succession, production, water use
Tree	10 ⁻² -10 ⁻³ m ²	Minutes-centuries	Phenology, reproduction, physiological processes, death

Vegetation modifies energy fluxes directly by altering the earth's albedo and indirectly by regulating greenhouse gases, especially CO₂, which absorb infrared radiation from the earth and thus create a warmer atmosphere (Mooney et al., 1987). A warmer atmosphere, in turn, should increase the rate of most biochemical processes including photosynthesis and respiration.

Biosphere water fluxes are also directly and indirectly affected by global vegetation. Evapotranspiration from vegetation directly alters the global hydrologic regime (Shuckla and Mintz, 1982). Global vegetation can indirectly affect biosphere water fluxes, in that a CO₂-controlled warmer atmosphere will cause a change in global precipitation patterns. Soil moisture availability will increase in some parts of the globe and decrease in others with a warmer climate. Global vegetation responses can be expected from these shifts in precipitation.

Recent human activities have affected these feedbacks between CO₂ concentrations, global climate, and global vegetation. The largest net global fluxes of carbon from 1800 to the present are the net releases of carbon due to land-use changes, particularly in the tropics

(Houghton et al., 1983; Mellilo et al., 1988), and from fossil fuel burning (Rotty, 1987). Extensive planting of forests has been proposed as one method for recapturing this "excess" CO₂ and thus slowing down climate change (Marland, 1988).

Biome

The major phenomena of interest within the biome paradigm are evolution/extinction and species migration. Changes in atmospheric CO₂ and climate are likely to affect the evolution and survival of tree species; however, these changes are difficult to predict. The genetic variability of CO₂-sensitivity is not known for any woody species, although differences among species have been documented (e.g., Tolley and Strain, 1984a,1984b). The high variability of other characteristics in natural populations and the fact that the early evolution of angiosperms took place in the Cretaceous era when atmospheric CO₂ concentrations were 3-10 times higher than today (Gammon et al., 1985) suggest that within-species variability in the response to CO₂ could be significant. Under rapidly changing environmental conditions, genetic shifts could occur within a few generations (Strickberger, 1985). The genetic resilience of most tree species to climate change

must be inferred from current climatic conditions within their natural ranges (Johnson and Sharpe, 1982). However, the boundaries of a species' range may reflect factors such as competitive ability rather than climatic constraints (Farr and Hard, 1987; Woodward, 1987, but see Michaels and Hayden, 1987 for an opposing view). Tree species with broad ranges, including most commercial species, are most likely to survive climate change. The many tree species that are rare or restricted in occurrence will be at greater risk of extinction.

Although rates of tree species migration in Europe and North America during the Ice Ages were ~300 m per year (Woodward, 1987), future migration rates are difficult to predict because the rate of a CO₂-induced climate change may be an order of magnitude faster than previous climate changes.

Furthermore, there will be new barriers to migration (cities, agriculture, roads) and new modes of migration (trains, cars, or transplants for horticulture or forest products). The current spatial distribution and abundance of a species will influence that species' ability to successfully migrate to regions of suitable climate and soils (Peters and Darling, 1985).

Human activities will greatly influence many biome forest responses. Breeding programs, a viable option for many commercial species, may permit certain species to maintain their current ranges (Kellison and Weir, 1987). Land-use and ownership will affect not only the migration rate of species but also their ultimate range and abundance. For example, the theoretical range of loblolly pine under a warmer climate would extend well into Indiana and Ohio (Solomon, 1986). However, the actual range would not extend that far north because the northern land would still be used for agriculture (Miller et al., 1987). Furthermore, the displacement of forest types in space will be likely to alter their ownership and thus their commercial productivity (Wallace and Newman, 1986). Human use

of forests for fuelwood could also change with a warmer climate, thereby altering rates of deforestation in some areas. The effectiveness of parks and wilderness areas in preserving rare species may change if the spatial distribution of a biome shifts. Humans may need to assist the migration of some species if these species are to survive (Peters and Darling, 1985). Active conservation is most likely to be necessary if the range of a species occurs at the edge of a biome, if the species has limited dispersal ability, or if the habitat of the species is disjointly distributed within the biome.

Ecosystem

Phenomena of special interest within the ecosystem paradigm are disturbance regimes and nutrient cycling. The frequency, duration, and severity of both abiotic and biotic disturbance regimes are likely to be altered by climate change and elevated CO₂. Abiotic disturbances such as fires and floods may change in frequency and intensity as a consequence of climate change. Forest fire frequencies should increase where the climate becomes warmer and drier (Sandenburgh et al., 1987; USDA Forest Service, 1987). The intensity and frequency of forest fires may also be altered by changes in species composition induced by elevated CO₂ and climate change. Flooding frequencies are also likely to change, although not unidirectionally (Tombaugh et al., 1982; USDA Forest Service, 1987). Many forest ecosystems are maintained by specific abiotic disturbances; a climate-induced shift in abiotic disturbances could by itself induce major ecosystem shifts (Johnson and Sharpe, 1982; Strain and Armentano, 1982).

Biotic disturbances such as forest pests and pathogens may also shift in response to elevated CO₂ and climate change. The ranges of pathogens are often limited by climatic factors (e.g., Rutherford and Webster, 1987), and their distribution may change. Insect herbivory may also increase because of CO₂-induced

changes in plant tissue quality (Butler et al., 1986; Lincoln et al., 1984). Of importance to managed forests and nature reserves are possible shifts in the range and relative competitiveness of weedy plants (Haynes, 1982; Peters and Darling, 1985).

Climate change and elevated CO_2 will also alter forest nutrient cycles by altering litter decomposition rates and tree nutrient uptake and internal cycling. Decomposition rates could change in response to climate and CO_2 -induced alterations in the physical environment, litter quality, or decomposer organisms. A warmer climate might increase the rate of decomposition by enhancing fungal and bacterial growth (Meentemeyer, 1978), but a drier climate would tend to retard decomposition. Forest arthropods, a key component of the decomposition process, could have their range altered and their activity level affected by changing plant tissue or litter quality (Cooper, 1982; Kimball, 1985). If the higher C:N ratio found in plant tissues grown under elevated CO_2 corresponds with a higher litter C:N ratio, then decomposition may be slowed because decomposition rates are negatively correlated with high litter C:N ratios (Mooney et al., 1987). However, there is experimental evidence that litter lignin:N ratios, which are also negatively correlated with decomposition rates and generally a better indicator of decay rates (Mellilo et al., 1982), remain the same or decrease under elevated CO_2 (Norby et al., 1986a). The interaction of all these positive and negative effects and the difficulties in extrapolating results across ecosystems limit our current ability to predict the overall impact of climate change and elevated CO_2 on decomposition processes. The impact of elevated CO_2 on many aspects of internal nutrient cycling is largely unknown. No studies have followed the effect of elevated CO_2 on woody plant nutrition for longer than one growing season. Limited data suggest that the return of nitrogen through litterfall may remain constant or decrease due to an observed increase in nutrient-use efficiency (Norby et al., 1986a). Species shifts

associated with elevated CO_2 and climate change may also change nutrient cycling patterns and rates at specific sites (Pastor and Post, 1988).

Human activities can modify ecosystem responses to climate change and elevated CO_2 . The impact of humans is most readily observed in human-induced disturbances such as pollution and introduced pests and in human modifications of natural disturbances through activities like fire suppression and flood control. Regional land-use changes could also influence forest ecosystem responses as an ecosystem's response to disturbance may be a function of its setting in the larger landscape.

Stand

Phenomena of interest within the forest stand paradigm are competition, succession, production, and water use. Competitive abilities of species may shift as a result of species-specific physiological responses to elevated CO_2 and climate change. Consequently, species compositions may change (Zangerl and Bazzaz, 1984). New species may invade, or species may be eliminated (Peters and Darling, 1985). Succession may proceed faster with a warmer climate or be slowed by drought conditions. Site-specific stand productivity could change because of changes in species composition, altered climate conditions for growth, or CO_2 fertilization effects (Leverenz and Lev, 1987). Stand water use, a critical factor in the hydrologic budgets of many regions, may decrease because individual tree water-use efficiency may increase with greater concentrations of atmospheric CO_2 (Leverenz and Lev, 1987; Miller et al., 1987). However, an increase in stand leaf area, because of CO_2 -enhanced growth and tolerance to shade, might counteract the decrease in stand water use expected from the improved water-use-efficiency.

Few studies empirically examine the relationship between stand properties and climate

across a wide sample of communities (Johnson and Sharp, 1982; but see Denton and Barnes, 1987), although site-specific empirical relationships between community parameters and climate have been developed using tree ring and pollen records (Cook et al., 1987; Josza and Powell, 1987; Webb, 1982; Woodward, 1987). Thus, it is difficult to predict in any quantitative sense how climate alone affects stand phenomena.

Experimental data on the impact of elevated CO₂ and climate change on stand phenomena are also sparse. A microcosm study of bottomland and upland tree communities, in which seedlings of different species were grown together for 90 days under elevated CO₂ and two levels of light, showed that elevated CO₂ had no effect on the overall growth of either community, although there were differential species responses to CO₂ within the communities (Williams et al., 1986). In another growth chamber study, a fast-growing pioneer tree species showed a 70 percent increase in biomass under an enriched CO₂ atmosphere, while a slower-growing climax species showed only a 30X increase (Oberbauer et al., 1985). Such studies suggest that successional paths may change and new community types may evolve under conditions of elevated atmospheric CO₂ just as they have in areas subjected to chronic ozone air pollution (Taylor, 1984).

Humans influence forest stands primarily through forest management activities, although local air and water pollution and poor soil management (erosion or compaction) can also be important. Silvicultural tools such as planting stock, density of planting, mulch, fertilization, and thinning regimes may be used in managed stands to counter negative effects of climate change or augment positive effects (Phares, 1980; Sandenburgh et al., 1987; Tombaugh et al., 1982). Forest response to elevated CO₂ and climate change may be easier to manage in mixed-species stands under uneven-aged management than in monospeci-

fic stands under even-aged management. Individual trees will respond to climate change on a gradual basis and at uneven rates. Uneven-aged management allows harvesting in accordance with the differential timing of those responses. In stands under even-aged management, species composition and genotype can be switched only at planting time. Thus, even-aged stands will require more decisive management with perhaps more risk. Already there is concern within the U.S. forest industry about the fate of loblolly pine stands planted to the south and west of their natural range if the climate in that region becomes even drier and hotter (Graham et al., 1986).

Trees

Phenomena of interest within the individual tree paradigm are phenology, life cycle events (e.g., reproduction, death) and physiological processes (e.g., photosynthesis, transpiration, respiration, carbon allocation, nutrient uptake, nutrient allocation). The key issue regarding each of these phenomena is to identify the effects of climate factors and/or atmospheric CO₂ with or without other stresses (e.g. drought, flooding, cold, shade, poor soil, pollution).

Our understanding of the effect of climate on trees is based largely on qualitative observations of mature trees and short-term (minutes to days) experiments on tree seedlings. In particular, there is very little information on how frequency of extreme climatic events affects tree phenomena (USDA Forest Service, 1987; World Meteorological Organization, 1985). This is especially important as climate change may frequently expose trees to climatic extremes that the trees are known to survive if subjected to only infrequently. The lack of experimental and quantitative data on mature trees hinders precision and accuracy in predictions on tree response to climate change.

Our understanding of the effect of CO₂ on

tree phenomena is limited to agricultural studies and short-term (< 2 growing seasons) studies on less than 20 tree species. Under well-watered and fertilized conditions, nearly all C_3 plants, including trees species, show significantly greater growth with the addition of elevated CO_2 (Kimball, 1986; Sionit and Kramer, 1986). The usefulness of this information is limited, however, as trees generally grow under less than ideal conditions and for many years. Thus, data on the long-term response to CO_2 under conditions of nutrient stress, water stress, and light deprivation are needed to predict the impact of elevated CO_2 on tree phenomena.

Existing short-term seedling studies suggest that elevated CO_2 will enhance seedling growth under conditions of nutrient, soil moisture, and light deprivation (Norby, 1987; Norby et al., 1986b; O'Neill et al., 1987; Tolley and Strain, 1984a, 1984b). The effects of temperature, humidity, or air pollution on the impact of elevated CO_2 on tree phenomena have not been studied, although agricultural studies

suggest that elevated CO_2 will mitigate negative responses to these factors (Kramer and Sionit, 1987). The lack of long-term studies precludes any data on tree life cycle events or phenology.

Humans can exert influence within this paradigm by modifying either the immediate environment of the tree (e.g., watering, fertilization, weed control, or pollution abatement) or the genetic makeup of the tree (e.g., breeding or genetic engineering). Of all the paradigms, this one is the most amenable to experimental study. Long-term data and data on phenological responses are especially needed at this time.

Linkages Between Paradigms

Linkages between these five paradigms are illustrated in Figure 1. The biome, community, and individual tree paradigms all consider species characteristics but at progressively finer spatial and temporal resolutions. In the same manner, biosphere, ecosystem, and individual

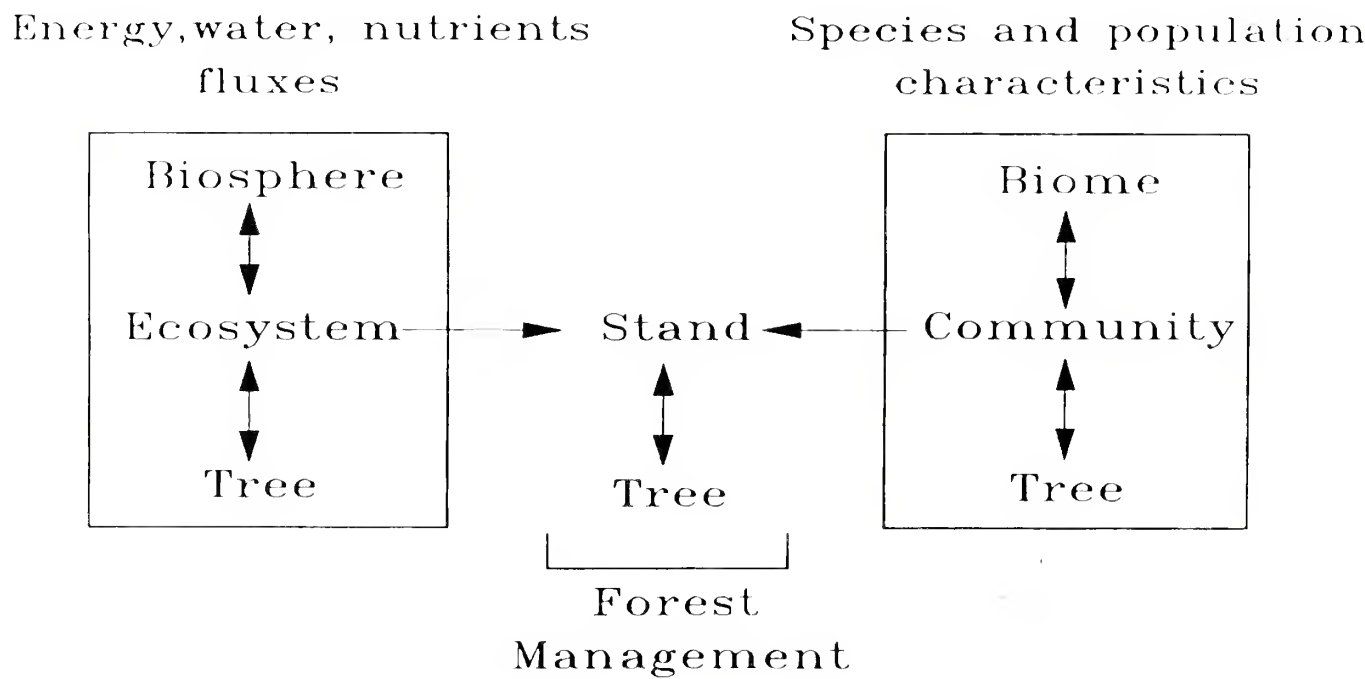


Figure 1. Interrelationships between biotic paradigms. The community paradigm, which was not expanded upon in his paper, is primarily at the same spatial and temporal scale as the stand and ecosystem paradigms. It encompasses the phenomena of succession and competition but in a more general sense in that the community paradigm is focused on all species, not just tree species.

tree paradigms all consider energy, nutrient, and water fluxes. The stand paradigm combines both the community and the ecosystem paradigm with a focus on management. It is important to recognize that these linkages are bidirectional across spatial and temporal scales. For example, succession, which takes decades or centuries and is part of the community and stand paradigm, is a function of (1) species-specific responses to environmental variables (measured at the individual scale), (2) competitive interactions among species for light, nutrients and water (measured at the community scale) and (3) seed source availability, which may be dependent on species migration rates (measured at the biome scale). Prediction of many forest phenomena will require both information collected across several spatial and temporal scales and the ability to link these scales.

Implications for Future Research

In developing future research, it is important to recognize and exploit the linkages between the five paradigms so that data and studies can be used most effectively. For example, data on litter quality, useful in making ecosystem predictions, can and has been collected in the course of individual tree studies (Norby et al., 1986a). Furthermore, the bidirectionality of the linkages between paradigms argues for forest response studies conducted within all paradigms. We cannot expect to predict the fate of forest resources if we focus on only one paradigm. The interconnectedness and the enormous spatial and temporal range of forest responses also stress the need for continued research on scaling problems, long-term field studies, and innovative models. Finally, the impact of human activity on forest responses must not be neglected, especially when studying forest responses within the stand and biome paradigms.

Literature Cited

- Butler, G. D. Jr., B. A. Kimball, and J. R. Mauney. 1986. Populations of *Bemisia tabaci* (Hymenoptera: Aleyrodidae) on cotton grown in open-top field chambers enriched with CO₂. *Environ. Entomol.* 15:61-63.
- Cook, E. R., A. H. Johnson, and T. J. Blasing. 1987. Forest decline: Modeling the effect of climate in tree rings. *Tree Physiol.* 3:27-40.
- Cooper, C. F. 1982. Food and fiber in a world of increasing carbon dioxide, pp. 299-320, *In* W. C. Clark (ed.), *Carbon Dioxide Review: 1982*. Oxford University Press, New York.
- Denton, S. R., and B. V. Barnes. 1987. Tree species distributions related to climatic patterns in Michigan. *Can. J. For. Res.* 17:613-629.
- Farr, W. A., and J. S. Hard. 1987. *Multivariate analysis of climate along the southern coast of Alaska—some forestry implications*. PNW-RP-372. USDA, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Gammon R. H., E. T. Sundquist, and P. J. Frazer. 1985. History of carbon dioxide in the atmosphere, pp. 25-62, *In* J. R. Trabalka (ed.), *Atmospheric Carbon Dioxide and the Global Carbon Cycle*. DOE/ER-0239. National Technical Information Service, Springfield, VA.
- Graham, R. L., T. R. Fox, and P. M. Dougherty. 1986. Multiple stress factors: The potential role of system models in assessing the impact of multiple stresses on forest productivity, pp. 151-170, *In* T.C. Hennessey, P. M. Dougherty, S. V. Kossuth, and J. D. Johnson (eds.), *Stress Physiology and Forest Productivity*. Martinus Nijhoff Publishers, Dordrecht, The Netherlands.
- Haynes, D. L. 1982. Effects of climate change on agricultural pests. Vol. II, Part 10 *In* *Environmental and Societal Consequences of a Possible CO₂-Induced Climate Change*. DOE/EV/10019-10. National Technical Information Service, Springfield, VA.
- Houghton, R. A., J. E. Hobbie, J. M. Mellillo, B. Moore, B. J. Peterson, G. R. Shaver, and G. M. Woodwell. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: A net release of CO₂ to the atmosphere. *Ecol. Monogr.* 53:235-262.

- Johnson, W. C., and D. M. Sharpe. 1982. Ecological consequences of CO₂-induced climatic change on forest ecosystems. Vol. II, Part 13 *In Environmental and Societal Consequences of a Possible CO₂-Induced Climate Change*. DOE/EV/10019-12. National Technical Information Service, Springfield, VA.
- Josza, L. A., and J. M. Powell. 1987. Some climatic aspects of biomass productivity of white spruce stem wood. *Can. J. For. Res.* 17:1075-1079.
- Kellison, R.C., and R.J. Weir. 1987. Breeding strategies in forest tree populations to buffer against elevated atmospheric carbon dioxide levels, pp. 285-294, In W.E. Shands and J.S. Hoffman (eds.), *The Greenhouse Effect, Climate Change, and U.S. Forests*. The Conservation Foundation, Washington, D.C.
- Kimball, B.A. 1986. Influence of elevated CO₂ on crop yield, pp. 106-115, *In* H.Z. Enoch and B.A. Kimball (eds.), *Carbon Dioxide Enrichment of Greenhouse Crops, Vol. II*. CRC Press, Boca Raton, Fl.
- Kimball, B.A. 1985. Adaption of vegetation and management practices to a higher carbon dioxide world, pp. 185-204, *In* B. R. Strain and J.D. Cure (eds.), *Direct Effects of Increasing Carbon Dioxide on Vegetation*. DOE/ER-0238. National Technical Information Service, Springfield, VA.
- Kramer, P.J., and N. Sionit. 1987. Effect of increasing carbon dioxide concentration on the physiology and growth of forest trees, pp. 219-246, *In* W.E. Shands and J.S. Hoffman (eds.), *The Greenhouse Effect, Climate Change, and U.S. Forests*. The Conservation Foundation, Washington, D.C.
- Leverenz, J.W., and D.J. Lev. 1987. Effects of carbon dioxide-induced climate changes on the natural ranges of six major commercial tree species in the western United States, pp. 123-155, *In* W.E. Shands and J.S. Hoffman (eds.), *The Greenhouse Effect, Climate Change, and U.S. Forests*. The Conservation Foundation, Washington, D.C.
- Lincoln, D.E., N. Sionit, and B.R. Strain. 1984. Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. *Environ. Entomol.* 13:1527-1530.
- Marland, G. 1988. *The prospect of solving the CO₂ problem through global reforestation*. DOE/NBB-0082. National Technical Information Service, Springfield, VA.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465-472.
- Mellillo, J.M., J.R. Fruch, and R.A. Houghton. 1988. Land-use change in the Soviet Union between 1850 and 1980: Causes of a net release of CO₂ to the atmosphere. *Tellus* 40B:116-128.
- Mellillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf decomposition dynamics. *Ecology* 63:621-626.
- Michaels, P.J., and B.P. Hayden. 1987. Modeling the climate dynamics of tree death. *Bioscience* 37:603-610.
- Miller, W. F., P. M. Dougherty, and G. L. Switzer. 1987. Effect of rising carbon dioxide and potential climate change on loblolly pine distribution, growth, survival, and productivity, pp. 157-187 *In* W. E. Shands and J. S. Hoffman (eds.), *The Greenhouse Effect, Climate Change, and U.S. Forests*. The Conservation Foundation, Washington, D.C.
- Mooney, H. A., P. M. Vitousek, and P. A. Matson. 1987. Exchange of materials between terrestrial ecosystems and the atmosphere. *Science* 238:926-932.
- Norby, R. J. 1987. Nodulation and nitrogenase activity in nitrogen-fixing woody plants stimulated by CO₂ enrichment of the atmosphere. *Physiol. Plant.* 71:77-82.
- Norby, R. J., J. Pastor, and J. M. Mellillo. 1986a. Carbon-nitrogen interactions in CO₂-enriched white oak: Physiological and long-term perspectives. *Tree Physiol.* 2:223-241.
- Norby, R. J., E. G. O'Neill, and R. J. Luxmoore. 1986b. Effects of atmospheric CO₂ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. *Plant Physiol.* 82:82-89.
- Oberbauer, S. F., B. R. Strain, and N. Fetcher. 1985. Effect of CO₂ enrichment on seedling physiology and growth of two tropical tree species. *Physiol. Plant.* 65:352-356.
- O'Neill, E. G., R. J. Luxmoore, and R. J. Norby. 1987. Elevated atmospheric CO₂ effects on seedling growth, nutrient uptake, and rhizosphere bacterial populations of *Liriodendron tulipifera* L. *Plant and Soil* 04:3-11.

- Pastor, J., and W.M. Post. 1988. Response of northern forest to CO₂-induced climate change. *Nature* 344(7):55-58.
- Peters, R. L., and J. D. S. Darling. 1985. The greenhouse effect and nature reserves. *Bioscience* 35:707-717.
- Phares, R. 1980. Impact of enhanced atmospheric CO₂ on managed forests, pp. 295-301, *In Environmental and Societal Consequences of a Possible CO₂-Induced Climate Change*. DOE Conf-7904143. National Technical Information Service, Springfield, VA.
- Rotty, R. M. 1987. Estimates of seasonal variation in fossil fuel CO₂ emissions. *Tellus* 39B:184 - 202.
- Rutherford, T. A., and J. M. Webster. 1987. Distribution of pine wilt disease with respect to temperature in North America, Japan, and Europe. *Can. J. For. Res.* 17:1050-1059.
- Sandenburgh, R., C. Taylor, and J. S. Hoffman. 1987. Rising carbon dioxide, climate change, and forest management: An overview, pp. 113-121, *In* W. E. Shands and J. S. Hoffman (eds.), *The Greenhouse Effect, Climate Change, and U.S. Forests*. The Conservation Foundation, Washington, D.C.
- Shuckla, J., and Y. Mintz. 1982. Influence of land-surface evapotranspiration on the earth's climate. *Science* 215:1498-1501.
- Sionit, N., and P. J. Kramer. 1986. Woody plant reactions to CO₂ enrichment, pp. 70-85, *In* H. Z. Enoch and B. A. Kimball (eds.), *Carbon Dioxide Enrichment of Greenhouse Crops, Vol II*. CRC Press, Boca Raton, FL.
- Solomon, A. M. 1986. Transient response of forests to CO₂-induced climate change: Simulation modeling experiments in eastern North America. *Oecologia (Berlin)* 68:567-579.
- Strain, B., and T. V. Armentano. 1982. Response of "unmanaged" ecosystems. Vol. II, Part 12 *In Environmental and Societal Consequences of a Possible CO₂-Induced Climate Change*. DOE/EV/10019-12. National Technical Information Service, Springfield, VA.
- Strickberger, M. W. 1985. *Genetics*. MacMillan Publishing, New York.
- Taylor, G. E. 1984. The significance of elevated level of ozone on natural ecosystems of North America, pp. 152-175, *In* S. D. Lee (ed.), *Evaluations of the Scientific Basis for Ozone/oxidants Standards*. Air Pollution Control Association, Houston, TX.
- Tolley, L. C., and B. R. Strain. 1984a. Effects of CO₂ enrichment on growth of *Liquidamber styraciflua* and *Pinus taeda* seedlings under different irradiance levels. *Can. J. For. Res.* 14:343-350.
- Tolley, L. C., and B. R. Strain. 1984b. Effects of atmospheric CO₂ and water stress on growth of *Liquidamber styraciflua* L. and *Pinus taeda* L. seedlings. *Can. J. Bot.* 62:2135-2139.
- Tombaugh, L. W., D. I. Dickman, and D. G. Sprugel. 1982. Direct effects of increased concentrations of atmospheric carbon dioxide on managed forests. Vol II, Part 7 *In Environmental and Societal Consequences of a Possible CO₂-Induced Climate Change*. DOE/EV/10019-7. National Technical Information Service, Springfield, VA.
- USDA Forest Service. 1987. *Forest productivity and health in a changing atmospheric environment: A Forest Service Priority Research Program*. Report by Forest Fire and Atmospheric Sciences Staff and Timber Management Staff, Forest Service, U.S. Dept. of Agriculture, Washington, D.C.
- Wallace, T. D., and D. H. Newman. 1986. Measurement of ownership effects on forest productivity in North Carolina from 1974 to 1984. *Can. J. For. Res.* 16:733-738.
- Webb, T. III. 1982. The use of paleoclimatic data in understanding and possible predicting how CO₂-induced climatic change may effect the natural biosphere. Vol II, Part 17 *In Environmental and Societal Consequences of a Possible CO₂-Induced Climate Change*. DOE/EV/10019-17. National Technical Information Service, Springfield, VA.
- Williams, W. E., K. Garbutt, F. A. Bazzaz, and P. M. Vitousek. 1986. The response of plants to elevated CO₂. IV. Two deciduous-forest tree communities. *Oecologia (Berlin)* 69:454-459.
- World Meteorological Organization. 1985. Impact on terrestrial ecosystems, pp. 62-66, *In Report of the International Conference on the Assessment of the Role of Carbon Dioxide and of Other Greenhouse Gases in Climate Variation*. WMO No. 661. World Meteorological Organization, Vienna, Austria.
- Woodward, F. I. 1987. *Climate and Plant Distribution*. Cambridge University Press, New York.
- Zangerl, A. R., and F. A. Bazzaz. 1984. The response of plants to elevated CO₂. II. Competitive interactions among annuals under varying light and nutrients. *Oecologia (Berlin)* 62:412-417.

Direct Responses of Forest Trees to Rising Atmospheric Carbon Dioxide¹

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The steadily increasing concentration of CO₂ in the atmosphere is one of the best documented changes occurring in the global environment. Forest resources can be expected to respond both to the direct effects of increased CO₂ and to the indirect effects of climate change arising from the "greenhouse effect" of CO₂ and other radiatively-active trace gases. Predictions about the indirect effects necessarily depend on a series of critical uncertainties about the relationships between fossil energy use and atmospheric CO₂, CO₂ and climate, climate and forests. Reliable speculation about the direct interaction between increasing atmospheric CO₂ and forest ecosystems will help resolve some of these uncertainties and improve our ability to evaluate the issue of global climate change.

The biosphere is both an important sink for atmospheric CO₂ and a source of CO₂. On a global basis, the fluxes of carbon between the biosphere and the atmosphere are to a significant degree determined by forest ecosystems, which account for about two-thirds of global

photosynthesis (Kramer, 1981). CO₂ is a primary substrate for photosynthesis and plant growth, and it has been well known for decades that photosynthesis is stimulated and plants grow larger or faster in CO₂-enriched environments. Such responses in trees could increase the flux of CO₂ from the atmosphere and subsequent sequestering of carbon in the biosphere, thereby slowing the rise in atmospheric concentration, even if forest clearing and burning simultaneously increases the countervailing flux of CO₂ to the atmosphere (Allen et al., 1987).

In addition to their role in the global carbon cycle, trees are an important commodity, and increased tree growth would be an economic benefit offsetting to some degree the various deleterious effects of climate change. Unlike annual crop plants, individual trees that are planted today will experience substantially higher concentrations of CO₂ during their lifetimes without the opportunity for genetic adaptation, whereas crop plants are constantly bred to perform best in the current CO₂ environment. Reliable information on the capacity for different

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tree species to respond to rising CO_2 and on the effect of elevated CO_2 on tree responses to climatic change could influence the decisions of forest companies on what species to plant in different regions in order to maximize productivity in an atmosphere different from the atmosphere of today.

Plant Responses to Elevated CO_2

Basic plant physiological processes (e.g., photosynthesis, transpiration, carbon metabolism, nitrogen metabolism) are similar in herbaceous plants and trees. The large body of literature on the responses of nonwoody plants to elevated CO_2 is, therefore, an appropriate starting point for considering the responses of woody plants. There are a number of comprehensive reviews on the responses of crop plants and grasses to elevated levels of atmospheric CO_2 (articles in Lemon, 1983; Strain and Cure, 1985; Enoch and Kimball, 1986) from which the following discussion is drawn. Surveys of the results of many experiments indicate that the growth of C_3 plants increases about 30% or more with a doubling of CO_2 concentration. A typical response to CO_2 enrichment is an increase in mass of all plant organs, with roots gaining proportionately more mass than stems, and stems more than leaves. The additional dry matter increases root length and produces both longer and thicker stems. Increases in leaf mass are associated with increases both in leaf area and thickness.

Physiological studies at the biochemical, organ, and whole-plant levels help to explain the plant growth responses to CO_2 enrichment. Photosynthesis increases in all plants on the initial exposure to elevated CO_2 . Starch often accumulates in leaves, which leads to an inhibition of photosynthesis in many species with longer-term exposures. Leaf transpiration rate decreases because of partial stomatal closure. Photorespiration is decreased, but dark respiration generally is not directly affected.

Symbiotic nitrogen fixation is enhanced in legumes

Despite the fundamental similarities among all green plants, trees have special attributes that are likely to influence how they respond to elevated CO_2 : large size, long life, and a predominance in unmanaged habitats with resource limitations. These attributes of trees also preclude many of the same kind of CO_2 enrichment experiments as have been accomplished with annuals. Inferential evidence, such as very short-term responses, responses of seedlings, or historical records must be used instead.

In several investigations, seedlings, trees, or parts of trees that have been growing in the ambient atmosphere have been subjected to sudden increases in CO_2 concentration. For example, Green and Wright (1977) enclosed shoots of *Pinus ponderosa* trees in cuvettes and exposed them to elevated CO_2 for 1 day. Photosynthesis was significantly enhanced. Wong and Dunin (1987) exposed a small group of trees in a 12-year-old *Eucalyptus* forest to 680 $\mu\text{l/l}$ CO_2 for 1 day in a 12-m high enclosure. Photosynthesis was 50% higher and transpiration was 30% lower, relative to a day 3 weeks prior at 340 $\mu\text{l/l}$ CO_2 . Such experiments may be quite useful for exploring fundamental questions concerning the mechanism of photosynthesis, and they have established that trees, like other green plants, do have the capacity for increased photosynthetic rates in elevated CO_2 levels. However, these instantaneous responses are not directly pertinent to the responses of trees experiencing a gradual enrichment of the atmosphere with CO_2 . The photosynthetic capacity of a particular leaf is influenced by carbon demand (sink strength) in other parts of the organism and by feedback inhibition from accumulation of metabolites in the leaf. The diurnal and seasonal patterns of photosynthesis may be more important than photosynthetic capacity. Canopy photosynthesis is also a function of leaf area development. Leaf area and tree growth are highly dependent

on past environmental conditions that alter the storage of metabolites and the number of leaf primordia.

Based in part on the limited predictive value of instantaneous responses to CO₂ enrichment, most studies on the effects of elevated CO₂ on trees have used seedlings or small saplings grown for all or most of their life in regulated CO₂ atmospheres in growth chambers or greenhouses. Generally, the responses are similar to those reported with herbaceous plants (Allen et al., 1987). Increased photosynthesis, decreased transpiration, increased dry matter accumulation, and other physiological, morphological, and phenological alterations have been documented in conifers, hardwood forest trees, fruit trees, and tropical trees (Enoch and Kimball, 1986; Kramer and Sionit, 1987).

Species vary in the magnitude or nature of their responses, but there is not yet a strong basis for classification by taxonomic relationships, growth form, or other characteristics. One obvious classification scheme would be deciduous versus evergreen (or broadleaf versus conifer), but results of such comparisons (e.g., between *Liquidambar styraciflua* and *Pinus taeda*) have been inconsistent (Tolley and Strain, 1984; Sionit et al., 1985). A species with a fixed growth habit (*Quercus alba*) might be expected to exhibit a smaller response to CO₂ enrichment than a free-growing species (*Liriodendron tulipifera*), at least during a single growing season, but this hypothesis has not been supported experimentally (Norby and O'Neill, 1988).

Resource Interactions

A major limitation on the use of most short-term studies as predictive tools for the responses of forest trees is that the plants were grown under constant, stress-free conditions, fully supplied with water and mineral nutrients. Forest trees grow in environments with multiple, interacting and fluctuating resources, and they commonly are subjected to water stress or a

limited nutrient supply. Competition between individuals in a stand further reduces resource availability. The CO₂ response of a tree seedling well supplied with water and nutrients may be a poor indication of the responses of forest trees to gradually rising atmospheric CO₂. Indeed, some physiologists and ecologists have suggested that resource limitations will preclude a growth response to elevated CO₂ and, therefore, discount the possibility of a direct effect of rising CO₂ on forests (Kramer, 1981; Strain and Cure, 1985). This invocation of the "law of the minimum" is overly simplistic in that it ignores the possible interactions between resources (Norby et al., 1986a; Kramer and Sionit, 1987).

Nutrients. Experiments at the Oak Ridge National Laboratory have explored the question of whether the growth of a tree in an infertile habitat will increase as the atmospheric CO₂ concentration rises. This research started with the general hypothesis that the stimulation of below-ground processes of plants grown in high CO₂ will increase nutrient availability, thereby circumventing current nutrient limitations to growth (Luxmoore, 1981). The various mechanisms proposed for CO₂ x nutrient interactions begin with high CO₂ stimulating photosynthesis. From what is known about carbon allocation patterns in plants, increased photosynthesis should lead to an increase in the relative amount of carbon translocated to root systems. This could give two kinds of response: a stimulation of activity per unit root, or an increase in root growth and exploration of the soil. In either case, nutrient uptake by the root system could be enhanced. Nutrient availability could also increase because of an increase in the exudation of carbon compounds from the root to the rhizosphere. This, in turn, could stimulate microbial activity involved in nutrient turnover. Symbiotic activity, such as mycorrhization or nitrogen fixation, might also increase. On the other hand, there are mechanisms that could lower the physiological demand for certain nutrients in high CO₂, that is, increase the plant's

nutrient-use efficiency.

Experiments in which tree seedlings were grown in pots containing nutrient-poor forest soil in controlled environment chambers with regulated CO₂ atmospheres have shown that nutrient deficiency does not preclude a growth response to elevated CO₂. For example, the growth of one-year-old *Quercus alba* seedlings that were severely N deficient was 85% greater in 690 µl/l CO₂ than in 362 µl/l CO₂ (Norby et al., 1986a), and N-deficient *Liriodendron tulipifera* in elevated CO₂ had 73% greater dry weight than plants in ambient CO₂ (O'Neill et al., 1987a). In both of these experiments plant growth increased without a concomitant increase in N uptake, suggesting an increase in N-use efficiency. Increased N-use efficiency in CO₂-enriched plants could result from a reduced activity of the enzyme ribulose biphosphate carboxylase/oxygenase, which accounts for a substantial portion of leaf N.

These and other experiments have also provided support for some of the proposed mechanisms whereby CO₂ enrichment might increase nutrient availability and uptake. In the aforementioned experiment with *Q. alba* seedlings, P uptake increased with CO₂ concentration, thereby maintaining an adequate concentration of P in the leaves, which is especially important since Conroy et al. (1988) have shown that if foliar P becomes deficient, a CO₂ growth response is inhibited (unlike the situation with N discussed above). The increased uptake of P in the *Q. alba* seedlings was attributed to accelerated P mineralization in the soil, which resulted from a greater proliferation of fine roots and associated mycorrhizae and rhizosphere bacteria (Norby et al., 1986a). A specific stimulatory effect of CO₂ on mycorrhization has been shown in several studies with the ectomycorrhizal species, *Q. alba* and *Pinus echinata* (O'Neill et al., 1987b; Norby et al., 1987). Symbiotic N₂ fixation was also shown to be stimulated by CO₂ enrichment in the leguminous species, *Robinia pseudoacacia* and the actinorhizal species,

Alnus glutinosa (Norby, 1987).

Water. The physiological responses of increased carbon assimilation and decreased transpiration in plants growing in elevated CO₂ lead to increased water-use efficiency, which should result in increased growth of plants with limited water supply (Morison 1985). There are many reports of elevated CO₂ increasing instantaneous transpiration efficiency in woody plants (Kramer and Sionit, 1987; Hollinger, 1987; Conroy et al., 1988), resulting from enhanced photosynthetic uptake, decreased transpiration (stomatal closure), or both. There are fewer reports documenting increased wholeplant water-use efficiency (Norby et al., 1986a; Conroy et al., 1988). In an experiment with *Liriodendron tulipifera* seedlings (Norby and O'Neill, 1988), CO₂ enrichment stimulated the rate of photosynthesis per unit leaf area, but this effect was compensated for by a decrease in the relative amount of leaf area. Although this reduction in relative leaf area limited the overall growth increase, it had favorable consequences for plant water use: the water-use efficiency of plants in elevated CO₂ was significantly higher than that in ambient CO₂.

Long-term Responses of Trees to Elevated CO₂

Another limitation of short-term CO₂ enrichment experiments is that they do not address the important attributes of the perennial habit and the problems of water transport and carbon balance in tall, massive trees. An experiment with an annual plant lasting several weeks or months might be considered a long-term experiment, but considering the importance in trees of the physiological functions associated with winter dormancy, carbon and nutrient storage and remobilization, and regrowth, CO₂ enrichment experiments with tree species should be called "long term" only if their duration exceeds one growing season. The long-term responses of woody plants to elevated CO₂ are just beginning to be addressed in

experimental studies. In a preliminary experiment in Livermore, California, seedlings and saplings of *Pinus ponderosa* were exposed to elevated CO₂ in open-top field chambers continuously for over 2 years (Surano et al., 1986). The treatments were unreplicated and there was only one sapling per treatment, but the results suggested that the beneficial effects of elevated CO₂ begin to decrease at concentrations greater than 500 µl/l. A long-term CO₂ enrichment study with *Liquidambar styraciflua* and *Pinus taeda* seedlings was initiated at the Duke University Phytotron (Kramer and Sionit, 1987), but only preliminary results have been reported. A long-term, replicated CO₂ enrichment study using *Quercus alba* and *Liriodendron tulipifera* seedlings in open-top field chambers will be initiated at the Oak Ridge National Laboratory in 1989.

Because of the difficulty and expense of long-term CO₂ enrichment experiments, other indirect approaches have been taken to analyze the responses of trees. Responses to historical increases in atmospheric CO₂ may be recorded in tree-ring chronologies. After statistically removing the influences of climate variables, LaMarche et al. (1984) attributed the anomalous increase in tree ring width of sub-alpine conifers to a direct response to the increasing concentrations of atmospheric CO₂. Another indirect approach was taken by Woodward (1987), who attributed the 40% decrease in stomatal density in the leaves of herbarium specimens of tree species collected over the last 200 years to the increase in atmospheric CO₂, although these results have been disputed by Korner (1988).

Forest Ecosystem Responses

Neither these historical records of past responses to CO₂ enrichment in mature trees nor direct experimentation with young trees over a few years enables us to predict with confidence the growth of trees in the CO₂-enriched atmosphere of the future. Beyond

direct observation of tree growth over the coming decades, a necessary approach will be to simulate tree growth with computer models. Physiologically-based simulation models are being constructed to address the responses of plants, including trees, to elevated CO₂ (Reynolds et al., 1988; Luxmoore et al., 1989). The use of a model based on the integration of physiological processes allows the prediction of plant growth responses under conditions beyond those used to calibrate the model, thus representing an approach to predicting the long-term response of a tree to elevated CO₂ from the short-term responses of seedlings. For this modeling approach to work, reliable data on the relevant physiological responses to CO₂ are required for model parameterization. The percentage dry weight increase of a seedling in a short-term experiment cannot be extrapolated to predict the dry weight increase in a mature tree under different conditions, but the physiological responses of a current-year leaf of a seedling can (with caution) be used to predict the response of a current-year leaf on a large tree. Many other measurements of short-term responses, such as the mass of dormant buds or nutrient storage in perennial tissue, may provide insights into the longer-term responses (Norby et al., 1986b).

The responses of forest ecosystems to elevated CO₂ will depend not only on the primary growth responses of individual trees, but also on diverse biotic and abiotic interactions (Strain, 1985). The dynamics of a forest stand over time have been simulated with computer models using generalized information about the birth, growth, and death of the individual species in the stand. This approach has been used to address the question of forest changes under different scenarios of CO₂-induced climate change (Solomon, 1986; Pastor and Post, 1988), but because of a lack of appropriate input data regarding the primary growth responses of different species or groups of species to CO₂ enrichment, the ecosystem modeling approach has been used only to a limited extent to address the direct effects of elevated CO₂ (Botkin,

1977; Solomon and West, 1987). As more information becomes available, either from long-term experiments or as output from physiological growth simulations, ecosystem models will be better able to incorporate CO₂ effects.

Ecosystem models incorporate response functions of trees to environmental resources as well as some feedbacks and interactions between tree growth and resource availability. Unless specific CO₂-response functions are included, however, the implicit assumption is that the interactions do not change with CO₂ concentration, despite the evidence from physiological studies that CO₂ concentration can influence resource availability and utilization. The model of Pastor and Post (1988), which simulates the responses of northern forest ecosystems to CO₂-induced climate change, emphasizes the importance of indirect effects on water availability, but it does not alter the relationship between tree growth and water as a function of CO₂ concentration. An increase in water-use efficiency is a well documented response to CO₂ enrichment, as discussed above. If longer-term experiments support the premise that increased water-use efficiency improves a tree's drought resistance, then this response should be incorporated into ecosystem models. Similarly, N availability, as controlled by litter decomposition, is an important component of ecosystem models (Pastor and Post, 1988). It has been suggested that CO₂ enrichment could alter the chemistry of leaf litter such that nutrient turnover will be slower (Strain, 1985). The available data (Norby et al., 1986b) do not support this premise, but more work can be done in relatively short-term experiments to provide the necessary input for modeling the long-term ecological response.

Given the potential importance of the direct responses of forest trees to increasing CO₂ and the difficulty in projecting the long-term responses from existing data, it is important that CO₂ enrichment experiments be designed to provide data that are relevant to longer-term

and ecological responses.

Literature Cited

- Allen, L.H., Jr., K.J. Boote, J.W. Jones, P.H. Jones, R.R. Valle, B. Acock, H.H. Rogers, and R.C. Dahlman. 1987. Response of vegetation to rising carbon dioxide: Photosynthesis, biomass, and seed yield of soybean. *Global Biogeochemical Cycles* 1:1-14.
- Botkin, D.B. 1977. Forests, lakes, and anthropogenic production of carbon dioxide. *BioScience* 27:325-330.
- Conroy, J.P., M. Kupperts, B. Kupperts, J. Virgonia, and E.W.R. Barlow. 1988. The influence of CO₂ enrichment, phosphorus deficiency and water stress on the growth, conductance and water use of *Pinus radiata* D. Don. *Plant Cell Environ.* 11:91-98.
- Enoch, H.Z., and B.A. Kimball, editors. 1986. *Carbon Dioxide Enrichment of Greenhouse Crops. Vol. II. Physiology, yield, and economics*. Boca Raton, FL: CRC Press, Inc.
- Green, K., and R. Wright. 1977. Field response of photosynthesis to CO₂ enhancement in ponderosa pine. *Ecology* 58:687-692.
- Hollinger, D.Y. 1987. Gas exchange and dry matter allocation responses to elevation of atmospheric CO₂ concentration in seedlings of three tree species. *Tree Physiol.* 3:193-202.
- Korner, C. 1988. Does global increase of CO₂ alter stomatal density? *Flora* (in press).
- Kramer, P.J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. *BioScience* 31:29-33.
- Kramer, P.J., and N. Sionit. 1987. Effects of increasing carbon dioxide on the physiology and growth of forest trees. In Shands, W.E., and J.S. Hoffman (eds.), *The Greenhouse Effect, Climate Change, and U.S. Forests*. Washington, DC: The Conservation Foundation. pp. 219-246.
- LaMarche, V.C., D.A. Graybill, H.C. Fritts, and M.R. Rose. 1984. Increasing atmospheric carbon dioxide: Tree ring evidence for growth enhancement in natural vegetation. *Science* 225:1019-1021.

- Lemon, E.R., editor. 1983. *CO₂ and plants: The response of plants to rising levels of atmospheric carbon dioxide*, AAAS Selected Symposium 84. Boulder, CO: Westview Press, Inc.
- Luxmoore, R.J. 1981. CO₂ and phytomass. *BioScience* 31:626.
- Luxmoore, R.J., M.L. Tharp, and D.C. West. 1989, in press. Modeling the physiological basis of tree ring response to environmental changes. In Dixon, R.K. (eds.), *Forest Growth: Process Modeling of Responses to Environmental Stress*. Auburn University, AL: Timber Press.
- Morison, J.I.L. 1985. Sensitivity of stomata and water use efficiency to high CO₂. *Plant Cell Environ.* 8:467-474.
- Norby, R.J. 1987. Nodulation and nitrogenase activity in nitrogen-fixing woody plants stimulated by CO₂ enrichment of the atmosphere. *Physiol. Plant.* 71:77-82.
- Norby, R.J., E.G. O'Neill, and R.J. Luxmoore. 1986a. Effects of atmospheric CO₂ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. *Plant Physiol.* 82:83-89.
- Norby, R.J., J. Pastor, and J.M. Melillo. 1986b. Carbon-nitrogen interactions in CO₂-enriched white oak: Physiological and long-term perspectives. *Tree Physiol.* 22:233-241.
- Norby, R.J., E.G. O'Neill, W.G. Hood, and R.J. Luxmoore. 1987. Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO₂ enrichment. *Tree Physiol.* 3:203-210.
- Norby, R.J., and E.G. O'Neill. 1988. Comparative responses of tulip-poplar and white oak seedlings to CO₂ enrichment of the atmosphere. Abstract; *Plant Physiol.* 86 (Suppl.):59.
- O'Neill, E.G., R.J. Luxmoore, and R.J. Norby. 1987a. Elevated atmospheric CO₂ effects on seedling growth, nutrient uptake, and rhizosphere bacterial populations of *Liriodendron tulipifera* L. *Plant Soil* 104:3-11.
- O'Neill, E.G., R.J. Luxmoore, and R.J. Norby. 1987b. Increases in mycorrhizal colonization and seedling growth in *Pinus echinata* and *Quercus alba* in an enriched CO₂ atmosphere. *Can. J. For. Res.* 17:878-883.
- Pastor, J., and W.M. Post. 1988. Response of northern forests to CO₂-induced climate change. *Nature* 334:55-58.
- Reynolds, J.F., R.L. Dougherty, J.D. Tenhunen, and P.C. Harley. 1988. PRECO: A model for the simulation of plant response to elevated CO₂. Washington, DC: U.S. Department of Energy, Carbon Dioxide Research Division, Office of Energy Research; Response of vegetation to carbon dioxide series report 042; 102 p.
- Sionit, N., B.R. Strain, H. Hellmers, G.H. Riechers, and C.H. Jaeger. 1985. Long-term atmospheric CO₂ enrichment affects the growth and development of *Liquidambar styraciflua* and *Pinus taeda* seedlings. *Can. J. For. Res.* 15:468-471.
- Solomon, A.M. 1986. Transient response of forests to CO₂-induced climate change: Simulation modeling experiments in eastern North America. *Oecologia* 68:567-579.
- Solomon, A.M., and D.C. West. 1987. Atmospheric carbon dioxide change: Agent of future forest growth or decline? In Titus, J.G. (ed.), *Effects of Changes in Stratospheric Ozone and Global Climate, Vol. 3: Climate Change*. Washington, DC: Proceedings, UNEP/EPA Conference. pp. 23-28.
- Strain, B.R. 1985. Physiological and ecological controls on carbon sequestering in terrestrial ecosystems. *Biogeochemistry* 1:219-232.
- Strain, B.R., and J.D. Cure, editors. 1985. *Direct Effects of Increasing Carbon Dioxide on Vegetation*. Washington, D.C.: U.S. Department of Energy; DOE/ER-0238; 286 p.
- Surano, K.A., P.F. Daly, J.L.J. Houppis, J.H. Shinn, J.A. Helms, R.J. Palassou, and M.P. Costella. 1986. Growth and physiological responses of *Pinus ponderosa* Dougl ex P. Laws to long-term elevated CO₂ concentrations. *Tree Physiol.* 2:243-259.
- Tolley, L.C., and B.R. Strain. 1984. Effects of CO₂ enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. *Can. J. For. Res.* 14:343-350.
- Wong, S.C., and F.X. Dunin. 1987. Photosynthesis and transpiration of trees in a eucalypt forest stands: CO₂ light and humidity responses. *Aust. J. Plant Physiol.* 14:619-632.
- Woodward, F.I. 1987. Stomatal numbers are sensitive to increases in CO₂ from pre-industrial levels. *Nature* 327:617-618.

Models for Analysis of Vegetation Responses to Global Environmental Change

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Abstract

The physiology of plants depends on temperature and moisture, thus large-scale climatic change can alter earth's vegetation. In turn, vegetation responses influence atmospheric composition and climate.

Maps of classical relationships between natural vegetation and climatic indices under alternate climates suggest the sensitivity of equilibrium vegetation distribution to climatic change. For example, 34 percent of the earth's 0.5° land cells are assigned different Holdridge Life-Zone designations under temperature increases simulated for a doubling of atmospheric CO₂ concentration. Although such exercises clarify the relative sensitivity of different types and regions and the scale of changes, the approach cannot be used to analyze transients.

Numerous variants of forest models that track the birth, growth, and mortality of each tree on relatively small stands simulate the dynamics of a range of forest types in terms of variables such as total biomass, species composition, and leaf area reasonably well. But individual plants are usually not important in larger scale applications. Models that describe population changes according to plant types without maintaining the state of each individual can simulate most of the large-scale features of vegetation dynamics.

Stand level models can be applied to large-scale problems by generating Monte Carlo solutions in which the distributions of parameter values reflect variability in environmental factors such as topography and soil characteristics. Random disturbances, such as fire and wind, can be incorporated as well. The solution

set reflects the combined influences of spatial variability in parameter values, disturbance, and variance induced by stochastic aspects of the models.

Introduction

Terrestrial vegetation is an important component of the global carbon cycle. There are approximately 560×10^{15} g of carbon in land plants; about 60×10^{15} g exchanged between the atmosphere and terrestrial ecosystems each year (Olson et al., 1983). These exchanges depend on temperature and moisture so that climatic change from increasing greenhouse gases – due in part to changes in terrestrial pools – can alter terrestrial storages and exchanges to feed back on the global biogeochemical cycles.

Environmental changes alter vegetation by affecting cell-level processes that depend on light, temperature, moisture, and nutrients; with time, the effects extend to variations in community characteristics, including species composition, biomass, and leaf profiles, and to the continental distributions of biomes. Atmospheric general circulation models describe the fast dynamics of the climate system, the response of circulation patterns to the boundary conditions imposed by solar radiation, atmospheric composition, and the instantaneous state of the land and water surfaces. But we also need to model slower components, including the response of the vegetation cover and surface hydrology to their boundary conditions: soil characteristics and longer-term values of atmospheric properties, such as mean air temperature, precipitation, and net radiation.

In this paper, we describe models for analyzing the equilibrium relationships between vegetation and climate and vegetation responses to environmental changes on time scales from 10-1000 years. We emphasize climate, but most of the concepts and approaches we present are pertinent to other

global changes as well.

Natural Processes of Vegetation Change

As plants respond to environmental change, competition for light and resources influence reproduction, growth, and mortality to different degrees, depending on each species' characteristics. As a result, variations in species composition, biomass, leaf area, and similar community variables are more complex than the collected responses of individuals that do not interact. There may be immediate effects on annual production, but these are modified later by changes in composition and community structure. This adjustment process is similar to secondary succession after disturbances such as fire or harvest.

Natural areas are mosaics of patches that were disturbed at different times by fire, wind, flood, disease, or similar events (Noble and Slatyer, 1978; White, 1979). Natural disturbance can quicken the response of vegetated areas to climatic change (Davis and Botkin, 1985), and presumably, harvest of wood or crops can have the same effect. Climatic change can alter disturbance regimes, e.g., warmer or drier conditions can increase fire frequency causing forest to be replaced by prairie (Grimm, 1984).

The availability of propagules for local recruitment depends on abundances in the surrounding area, and at this level, climatic change can alter regional distributions of taxa. Such changes are well documented for the past 20,000 years (Davis, 1981; Huntley and Birks, 1983; Webb, 1986; Webb, 1987). Trees migrated with remarkable speed in response to Quaternary changes, but the time needed for large-scale spread and regional population changes may be 1,000 years or more and can presumably limit the rate of vegetation response to rapid, large climatic changes (Davis et al., 1986; Bennett, 1986; Davis, 1987).

Vegetation and soil are tightly coupled systems. Soil water holding capacity and nutrient availability in the soil-water solution influence primary production. Although some aspects of soil formation are slow enough to be considered constant through plant community changes, nutrient turnover depends on litter characteristics so that variations in species composition can affect plant growth and further alter composition (Pastor and Post, 1986). The effects of climatic change may be amplified through this indirect circuit of influence (Pastor and Post, 1988).

Thus, in the face of climatic change, vegetation has a certain inertia (Smith, 1965), comprised of several components: (1) the time needed for individual patches of vegetation to adjust to climatic change when the available flora is held constant, (2) time for the spatial mosaic of vegetation to adjust to climatically induced changes in frequencies of fire and other natural hazards, and (3) the time required for ecdysis.

Equilibrium Relationships

The natural, equilibrium distribution of vegetation is similar to climate, and plant geographers use this correlation to relate vegetation classes to climate (Holdridge, 1947; Box, 1981; Lashof, 1987; Woodward, 1987). Sensitivity tests of such models suggest bounds on the impacts of climatic change.

Emanuel et al. (1985a,b) compared two world maps of Holdridge life zones: the first derived from climate recorded by 7000 meteorological stations, the second with simulated temperature increases for atmospheric CO₂ concentration twice the model reference concentration. Lashof (1987) did similar exercises with a vegetation-climate relationship derived from Olson's world map of ecosystem complexes (Olson et al., 1983) and meteorological records. Although the transient responses would be complex (Shugart et al., 1986; Solomon,

1986), such tests indicate the sensitivity of the asymptotic distributions toward which transients eventually converge in the absence of disturbances not included in these equilibrium relationships.

In this sensitivity test, the life-zone designations of 35 percent of the 0.5° mapping cells change. The largest changes were at high latitudes where simulated temperature increases are largest and where narrow temperature intervals define Holdridge life zones. The extents of boreal forests and tundra decrease 37% and 32% respectively. Changes are along major vegetation boundaries and are more extensive than the uncertainty in determining these boundaries within the Holdridge scheme.

Such speculations indicate some of the challenges agriculture and forestry may face and bound the broad vegetation changes that influence the global carbon cycle, climate, and other earth systems. But environmental changes due to human activities may be rapid compared to the vegetation dynamics responsible for replacement of forest types. Although the sensitivity of the Holdridge scheme suggests conversion of much of today's boreal forest to temperate deciduous forest, this result does not mean that there is likely to be a gradual, straightforward transition between the two forest types.

Higher summer temperatures may stimulate the growth of boreal conifers at first, but higher winter temperatures may be unfavorable for the natural regeneration of some of these taxa at their oceanic limits. Beyond a certain point, increased summer temperature will reduce growth rates again; such a warm climate would probably be suitable for temperate trees, but their recruitment will take time, so production could fall before rising again toward the high level characteristic of temperate forests.

Community Models

Various models describe vegetation tran-

sient responses from different viewpoints. Forest stand growth and succession models (Botkin et al., 1972; Ek and Monserud, 1981; Shugart, 1984) simulate changes based on species attributes and tree interaction assumptions that emphasize competition for light. These relatively new models borrow many ideas from forestry models (Munro, 1974). Nonwoody vegetation dynamics can probably be treated with similar descriptions, and although these models describe small landscape patches, they simulate community phenomena with considerable generality and use factors to describe environmental influences that can be evaluated along gradients or to sample variability within larger landscape units.

Shugart (1984) describes forest stand models and their application in detail. These models simulate the birth, growth, and death of every tree on a small stand (800 m²). The size of each tree is characterized by its diameter - other dimensions are allometrically related to diameter, and variables such as biomass can be derived from diameter using empirical functions.

To advance a simulation through one-year steps, a diameter increment is calculated for each tree:

$$\Delta D = \frac{r l_a (D_m H_m - (137.0D + b_2 D^2 - b_3 D^3))}{D_m H_m (274.0D + 3b_2 D^2 - 4b_3 D^3)} g_1(\phi) g_2(G_D) \quad (1)$$

D is diameter at 137 cm high. Leaf area l_a is a function of diameter

$$l_a = a d^b \quad (2)$$

The constants a and b are derived from relationships developed by Sollins et al. (1973):

$$\begin{aligned} a &= 1.6069 \times 10^4 \\ b &= 2.129. \end{aligned}$$

r is a growth rate, and D_m and H_m are maximum

diameter and height. These three parameters are specific to each tree species. The species specific functions $g_1(\phi)$ and $g_2(G_D)$, described below, express dependence on light and a heat sum G_D respectively. Additional response functions may be included to treat moisture, nutrient availability, and other environmental conditions.

Height is related to diameter by the function:

$$H = 137 + b_2 D - b_3 D^2 \quad (3)$$

where again the parameters b_2 and b_3 are species specific. If maximum height is assumed to occur at maximum diameter,

$$b_2 = 2(H_m - 137)/D_m \quad (4)$$

and

$$b_3 = (H_m - 137)/D_m^2 \quad (5)$$

Light intensity decreases below the top of the plant canopy because of shading. This affects growth through the light response function $g_1(\phi)$ in the diameter-increment equation, Eq. (1), and may affect other processes, such as recruitment. Shading is the most important interaction between trees in stand models. Light extinction is described by Beer's Law (e.g., Miller, 1981): at height H, intensity ϕ is

$$\phi(H) = \phi_0 e^{-k \int_H^\infty l_i(h) dh} \quad (6)$$

where ϕ_0 is the intensity at the top of the canopy, and k_i is a constant light extinction coefficient. $l_i(H)$ is the leaf-area index (leaf area/patch size) at height H.

Leaf area is directly related to stem diameter and considered to be concentrated at the top of the stem, thus the total leaf area of each tree shades all tree below. Stand models treat a plot of definite size that is constrained by the assumption that light availability is independent of

horizontal position (Shugart and West, 1979). Shugart and West (1977) simulated gap dynamics in an east Tennessee temperate forest on a 833 m² plot. But in boreal forests, tree crowns are narrow, sun angles are low, and the gap created by the death of a single tree is insignificant. Leemans and Prentice (1987) found that to simulate gap processes, models of these forests must be able to treat 1000 m² gaps for establishment of light-demanding species (Whitmore, 1982).

The dependence of diameter increment on light intensity is expressed by the response function $g_1(\phi)$. A typical light response function is

$$g_1(\phi) = c_1(1 - e^{c_2(\phi - c_3)}). \quad (7)$$

The parameters c_1 , c_2 , and c_3 reflect the shade tolerance of each species.

Temperature during the growing season is summarized by a growing degree-days index:

$$G_D = \sum_{i=1}^{365} ((T_i - T_B), T_i > T_B), \quad (8)$$

where T_i is daily temperature. T_B is a base temperature (e.g., 14.4°C or 40°F). This index affects diameter increment through the response function $g_2(G_D)$:

$$g_2(G_D) = \frac{4(G_D - G_D^{\min})(G_D^{\max} - G_D)}{(G_D^{\max} - G_D^{\min})}, \quad (9)$$

where G_D^{\max} and G_D^{\min} are maximum and minimum values of the growing degree-days index associated with each species' range.

Additional environmental effects can be described by similar response functions $g_i(.)$ multiplying growth increment, Eq. (1), to reflect deviations from best conditions. Winter cold is indexed by the mean temperature of the coldest month; growth is suppressed if it is too cold. Drought is described by an estimate of the proportion of the growing season with subcriti-

cal soil moisture. Growth is reduced to zero if drought index is less than or equal to the arid range limit for each species, determined from distribution maps. Bonan's (1988) boreal forest model considers the response of each species to permafrost. Pastor and Post (1986) constrain growth by nitrogen availability.

The environmental response functions depend on indices (e.g., drought index) that in turn are functions of environmental variables such as temperature or soil moisture. Some of these, such as temperature, are specified directly or treated as random variables with specified distributions. Others, such as soil moisture, are functions of additional variables including perhaps the status of model vegetation, and these relationships are described by environmental submodels whose state variables may depend on vegetation variables.

Randomly selected trees are eliminated from the model stand on each time step. The probability that a tree dies is much higher if it is suppressed than if it is growing well. The probability of mortality for all trees is such that fewer than 2 percent of the recruits of each species reach maximum age. If the annual diameter increment is below a critical value for three years running, a tree is considered slow growing and is assigned 1 percent probability of surviving the next ten years.

Disturbances such as fire and wind also affect mortality (Mielke et al., 1978; Shugart and Noble, 1981; Doyle, 1981). Their occurrence and intensity are usually random variables and may depend on environmental conditions such as temperature or moisture. These relationships are described by additional modules when a model is assembled for a region where they are important. Mortality associated with disturbance can be immediate – trees are removed from the model stand in the year disturbance occurs. In other cases, the probability of death may be increased according to species' tolerance. Disturbance can affect growth by de-

creasing diameter increment.

Random numbers of new trees are recruited annually as saplings for each species whose regeneration requirements – including light at the forest floor, mineral soil exposure, and leaf-litter depth – are met by environmental and vegetation status. The persistence of species is assured by an assumed constant propagule bath (Whittaker and Levin, 1977).

Forest models based on the Botkin formulation are uniquely successful in describing stand dynamics on time scales ranging from decades to centuries. But a model that describes population changes for each species or even plant types, as opposed to treating individuals, may be satisfactory for most continental- to global-scale applications. The computational requirements of population based models can be substantially less than those of models that track individuals.

One possibility is to describe the state of plant communities by the number of individuals of each species or plant type in each of a set of arbitrary width layers dividing space above the landscape unit supporting the vegetation. Again, the patch is sufficiently small so that light extinction can be assumed to be horizontally homogeneous.

Advancement through height layers is a stochastic process. The probability of transfer to higher layers is derived from a mean height increment of the population of each plant type, assumed to be uniformly distributed through each layer. The increment depends on current leaf size as well as environmental conditions including available light, air temperature, and soil moisture. The structural emphasis on height and the assumption of homogeneity within height layers for each plant type or species are conducive to incorporating plant types other than trees for which a growth description based on individuals is unnatural.

Large-Scale Analysis

Continental-scale simulations of vegetation dynamics can be generated from large sets of patch model solutions. The region of interest is subdivided. A uniform grid in spherical coordinates is convenient, but arbitrary polygons can be used. Resolutions of about 0.5° are reasonable (Olson et al., 1983; Emanuel et al., 1985); such cells are approximately 50 km on a side at the equator.

A set of patch model solutions is generated for each of these smaller units with appropriately distributed random environmental variables. Disturbance frequency and intensity are also specified—they may depend on environmental characteristics such as temperature or soil moisture as well as the status of vegetation (Kercher and Axelrod, 1984). The solution set reflects specified variances in environmental variables, including disturbance frequency and intensity, but is complicated by the stochastic processes simulated by the patch model.

For land units small enough to support reasonable resolution, the distributions of basic environmental variables, such as temperature, rainfall, soil type, and soil texture, cannot be derived from currently available observations. Rather, the distribution of these variables must be based on morphologic features with topography as the most important.

There are models for calculating solar intensity at a specified location, elevation, slope, aspect, and time (Swift, 1976; Bonan, 1988; Kutzbach and Gallimore, 1988). Although basic principles are understood for other relations, for example temperature change as a function of elevation, these have not yet been expressed systematically in schemes suitable for incorporation in global vegetation models. It is important to note that absolute relationships are not required; rather we need to derive the distributions of environmental variables from underlying variability in topography and other structural

characteristics.

Conclusion

Those wishing to study interactions between climate and ecosystems must reconcile the different spatial and temporal scales of atmospheric and ecological processes. The design of atmospheric general circulation models reflects the fast horizontal transport and short memory of the atmosphere - integrations are performed at intervals of less than an hour and at grid points 200 km, or more, apart. Vegetation models are solved on yearly intervals but on patches about 30 m across. These differences reflect the inertia of vegetation and the fine spatial scales at which vegetation processes act compared to those determining weather.

There are general circulation models that allow a prescribed vegetation, in terms of height, structure, phenology, rooting depth, etc., to interact dynamically with the atmosphere (Dickinson, 1984; Sellers et al., 1986). Physical vegetation characteristics, such as albedo, leaf-area index, and stomatal aperture, vary diurnally and seasonally in response to atmospheric variables and, in turn, affect exchanges of energy, water, and momentum. The task of a global vegetation model is to simulate the slower processes by which primary vegetation characteristics - taken as constant in climate models - are transformed through time by changes in climate.

We've described the components of a scheme for simulating global transient responses of natural vegetation to climatic change. The approach is based on a core description that in our experience simulates the important processes reasonably well. Substantial data are required to estimate model parameters for world-scale studies, but these needs are realistic. Simulations of vegetation responses within hypothetical environments can make substantial contributions toward understanding the implications and impacts of climatic change.

Adequate data are available now to support realistic continental-scale simulations for most of the world's land areas, but data limitations always restrict the interpretation of such large-scale efforts to some degree. Our ability to interpret realistic model studies can be extended substantially by hypothetical simulations.

Literature Cited

- Bennett, K.D. 1986. The rate of spread and population increase of forest trees during the postglacial. *Philosophical Transactions of the Royal Society of London*, B 314:523-531.
- Bonan, G.B. 1988. *A Simulation Model of Environmental Processes and Vegetation Patterns in Boreal Forests: Test Case Fairbanks, Alaska*. WP-88-63. International Institute for Applied Systems Analysis, Laxenburg, Austria.
- Botkin, D.B., J.F. Janak, and J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60:849-873.
- Box, E.O. 1981. *Macrocclimate and Plant Form*. Junk, The Hague, The Netherlands.
- Davis, M.B., and D.B. Botkin. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. *Quaternary Research* 23:327-340.
- Davis, M.B. 1981. Quaternary history and the stability of forest communities. pp. 132-153. In D.C. West, H.H. Shugart, and D.B. Botkin (eds.) *Forest Succession: Concepts and Application*. Springer-Verlag, New York.
- Davis, M.B. 1987. Invasion of forest communities during the Holocene: Beech and hemlock in the Great Lakes region. pp. 373-394. In A.J. Gray, M.J. Crawley, and P.J. Edwards (eds.). *Colonization, Succession, and Stability*. Blackwell, Oxford.
- Davis, M.B., K. D. Woods, S.L. Webb, and R.B. Futyma. 1986. Dispersal versus climate: Expansion of *Fagus* and *Tsuga* into the upper Great Lakes region. *Vegetatio* 67:93-103.

- Dickinson, R.E. 1984. Modeling evapotranspiration for three-dimensional global climate models. pp. 58-72. In J.E. Hansen, and T. Takahashi (eds.). *Climate Processes and Climate Sensitivity*. Geophysical Monograph 29. American Geophysical Union, Washington, D.C.
- Doyle, T.W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. pp. 56-73. In D.C. West, H.H. Shugart, and D.B. Botkin (eds). *Forest Succession: Concepts and Application*. Springer-Verlag, New York.
- Ek, A.R., and R.A. Monserud. 1981. Methodology for modeling forest stand dynamics. pp. 177-184. In D.E. Reichle (ed.). *Dynamic Properties of Forest Ecosystems*. Cambridge University Press, London.
- Emanuel, W.R., H.H. Shugart, and M.P. Stevenson. 1985a. Climatic change and the broad-scale distribution of ecosystem complexes. *Climatic Change* 7:29-43.
- Emanuel, W.R., H.H. Shugart, and M.P. Stevenson. 1985b. Response to comment: Climatic change and the broad-scale distribution of ecosystem complexes. *Climatic Change* 7:457-460.
- Grimm, E.C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* 54:291-311.
- Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.
- Huntley, B., and H.J.B. Birks. 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0-13,000 Years Ago*. Cambridge University Press, Cambridge.
- Kercher, J.R., and M.C. Axelrod. 1984. A process model of fires, ecology, and succession in a mixed-conifer forest. *Ecology* 65:1725-1742.
- Kutzbach, J.E., and R.G. Gallimore. 1988. Sensitivity of a coupled atmosphere/mixed layer ocean model to changes in orbital forcing at 9000 years B.P. *Journal of Geophysical Research* 93:803-821.
- Lashof, D.A. 1987. *The Role of the Biosphere in the Global Carbon Cycle: Evaluation Through Biospheric Modeling and Atmospheric Measurement*. Ph.D. Dissertation, University of California, Berkeley.
- Leemans, R., and I.C. Prentice. 1987. Description and simulation of tree-layer composition and size distributions in a primeval *Picea-Pinus* forest. *Vegetatio* 69:147-156.
- Mielke, D.L., H.H. Shugart, and D.C. West. 1978. A Stand Model for Upland Forests of Southern Arkansas. ORNL/TM-6225. Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Miller, D.H. 1981. *Energy at the Surface of the Earth*. Academic Press, New York.
- Munro, D.D. 1974. Forest growth models. A prognosis. pp 7-21. In J. Fries (ed.). *Growth Models for Tree and Stand Simulation*. Research Notes 30. Department of Forest Yield Research, Royal College of Forestry, Stockholm.
- Noble, I.R., and R.L. Slatyer. 1978. The effect of disturbance on plant succession. *Proceedings of the Ecological Society of Australia* 10:135-145.
- Olson, J.S., J.A. Watts, and L.J. Allison. 1983. *Carbon in Live Vegetation of Major World Ecosystems*. ORNL-5862. Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2:3-27.
- Pastor, J., and W.M. Post. 1988. Response of northern forests to CO₂-induced climate change. *Nature* 344:55-58.
- Sellers, P.J., Y. Mintz, Y.C. Sud, and A. Dalcher. 1986. A simple biosphere model (SiB) for use within general circulation models. *Journal of the Atmospheric Sciences* 43:505-531.
- Shugart, H.H. 1984. *A Theory of Forest Dynamics*. Springer-Verlag, New York.
- Shugart, H.H., and I.R. Noble. 1981. A computer model of succession and fire response of the high-altitude *Eucalyptus* forest of the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology* 6:149-164.
- Shugart, H.H., Jr., and D.C. West. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *Journal of Environmental Management* 5:161-179.

- Shugart, H.H., and D.C. West. 1979. Size and pattern of simulated forest stands. *Forest Science* 25:120-122.
- Shugart, H.H., M.Y. Antonovsky, P.G. Harvis, and A.P. Sandford. 1986. CO₂, climatic change and forest ecosystems. pp. 475-521. In B. Bolin, B.R. Doos, J. Jager, and T.A. Warrick (eds.). *The Greenhouse Effect, Climatic Change, and Ecosystems*. SCOPE 21. John Wiley, Chichester.
- Smith, A.G. 1965. Problems of inertia and threshold related to post-glacial habitat changes. *Proceedings of the Royal Society, B* 161:331-342.
- Sollins, P., D.E. Reichle, and J.S. Olson. 1973. *Organic Matter Budget and Model for a Southern Appalachian Liriodendron Forest*. EDGB/IBP-73/2. Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Solomon, A.M. 1986. Transient response of forests to CO₂-induced climate change: Simulation modeling experiments in eastern North America. *Oecologia* 68:567-579.
- Swift, L.W., Jr. 1976. Algorithm for solar radiation on mountain slopes. *Water Resources Research* 12:108-112.
- Webb, T., III. 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* 67:75-92.
- Webb, T., III. 1987. The appearance and disappearance of major vegetation assemblages: Long-term vegetational dynamics in eastern North America. *Vegetatio* 69:177-187.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229-299.
- Whitmore, T.C. 1982. On pattern and process in forests. pp. 45-60. In E.I. Newman (ed.). *The Plant Community as a Working Mechanism*. Blackwell, Oxford, U.K.
- Whittaker, R.H., and S.A. Levin. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12:117-139.
- Woodward, F.I. 1987. *Climate and Plant Distribution*. Cambridge University Press, Cambridge, U.K.

Brief Reports

Geographic Information Systems as a Tool in Regional Mapping and Environmental Assessment

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The U.S. Environmental Protection Agency's (USEPA) Direct/Delayed Response Project (DDRP) is examining the following question: "What is the future long term chemical response of selected surface waters in the U.S. to acidic deposition?" To answer this question, the USEPA, in cooperation with other Federal agencies and extramural investigators, compiled and/or collected a variety of environmental data encompassing selected regions of concern within the eastern U.S. We chose an ARC/INFO* Geographic Information System (GIS) as an appropriate tool for compilation, manipulation, and displaying of data and results obtained in the DDRP. GIS-based graphic output includes locational maps, contour maps, circle

and thiessen maps, and choropleth maps. This output aids researchers in many aspects of the DDRP including locational and logistical support, analyses, and communication of results. In particular, the interactive environment of GIS graphics allows researchers to examine numerous 'what if' scenarios. These GIS-generated datasets and maps are being used in a variety of procedures and predictive models to characterize the chemical response of surface waters in the regions of concern.

*Mention of brand names or commercial products does not constitute endorsement or recommendation for use.

Fluoride Emission and Tree Growth

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Fluoride emissions from the aluminum smelter at Kitimat, B.C., Canada, have been affecting the adjacent forests since 1954. Continuing studies of this effect have been conducted since 1973. Fluoride emission of the aluminum smelter at Kitimat has reduced forest

growth near the smelter, but satisfactory natural regeneration has taken place throughout the same area. The level of fluoride emission has dropped as emission control technology has improved markedly over the last decade and trees have responded with increased growth.

Geographic Information Systems as a Tool in Watershed Characterization for Regional Environmental Assessment

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The Direct/Delayed Response Project examines the following question: "What is the future long term chemical response of surface waters to continued acidic deposition?" The USEPA contracted soil scientists to map soils, vegetation, geology, and depth-to-bedrock on 145 watersheds in the northeast and 35 watersheds in the Southern Blue Ridge Province. These maps were digitized into an ARC/INFO Geographic Information System (GIS) and are currently being used to characterize watersheds

on both a per-watershed and regional basis. Characterization involves a variety of tasks including: characterization of individual layers, aggregation of mapping units within and between layers, and identification of mapping units in certain proximities of the study lake or stream reach. GIS-generated datasets and/or maps, based on these characterizations, are being used in a variety of procedures and predictive models to assess the influence of key watershed variables on surface water chemistry.

Quality Assurance Guidelines for Dendrochronological Research Projects

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A properly designed Quality Assurance (QA) program should perform two functions. First it should provide benefits to each research project, for example, a system of activities by which a set of standard operating procedures is selected, a knowledge of errors due to sample processing is accumulated, and an error-free data set is produced for analysis. Second, a QA program should provide the data users with specialized information for evaluating the level of certainty of scientific results that may be used to formulate environmental policy. This second function can be accomplished only if each proj-

ect conducts proper QA activities and documents them thoroughly.

This poster presents guidelines for conducting and documenting QA activities in dendrochronological research projects. Good use of these guidelines is illustrated with selected examples from projects funded by the Western Conifers Research Cooperative of the Forest Response Program. The work of L. Brubaker, D. Graybill, and D. Peterson and their staffs is acknowledged.

Mapping of Soils on Watersheds Selected to Represent a Region of Environmental Concern

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Watersheds were selected to statistically represent a region of concern in which to predict how many surface water systems will become acidic due to acidic deposition, and on what time scale. Regional soil surveys were conducted to provide information on the occurrence of soils and other characteristics on these watersheds. Soils were mapped at second order intensity and a scale of 1:24,000. Soils across several states were mapped and correlated to one

unified legend so that soil classes could be characterized for the region. The mapping design provided a database that described the spatial distribution of soils and other watershed characteristics within a watershed, correlated map unit composition and soils within the region, and allowed for extrapolation of results across the region of concern. All mapped information was entered on a geographic information system for retrieval and analyses.

Free Radical Adducts of Chloroplast and Nuclear DNA in Ozone and UV-B Exposed Plants¹

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Hydroxyl free radicals react with DNA to form several products, one of which is 8-hydroxyguanine. Enzymatic digests of DNA contain the altered nucleoside, 8-hydroxy-2-deoxyguanosine (8-OHdG), which can be precisely measured by HPLC electrochemical detection. Using this method, we found that the 8-OHdG content of chloroplast DNA is greater in bush beans and peas grown under a variety of ozone exposures known to induce plant injury. Exposure of illuminated isolated chloroplasts to ozone

caused nearly a 7-fold increase in 8-OHdG in the chloroplast DNA over the non-ozone exposed controls. Isolated DNA solubilized in buffer and exposed to ozone did not yield higher levels of 8-OHdG, though the ozone reacted with DNA per se as assessed by absorbance at 260nm. Currently, we are investigating ozone- and UV-B-related elevation of 8-OHdG in conifer, aspen and rice chloroplast DNA and determining if there is nucleotide specificity in ozone- or UV-B-induced damage to chloroplast DNA.

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An Analysis of the Reliability of DBH Measurement

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Defensible assessment of air pollution impacts on forests depend upon precise and accurate measures of tree growth and yield. Diameter breast height (DBH) is a fundamental measure of tree size and, almost universally, DBH measurements are taken with either diameter (actually girth) tapes or with mechanical calipers. Unfortunately, little is known about the absolute and differential errors of measurement associated with these techniques. Much of the difficulty derives from the ill-defined nature of the diameter of a noncircular cross-section such as a tree stem. Therefore, it is extremely difficult to gauge the quality and comparability of DBH

data between investigations and between techniques, especially when the likely and confounding influence of operator error is recognized.

The size of these errors may be critical in differentiating between changes due to measurement error and possibly subtle forest growth changes due to pollution exposures. In this study, variance component models are proposed to quantify the variability in basal area measurements in order to determine the most reliable means of taking repeated DBH measurements.

Relationships Among Mapped Watershed Physical Characteristics and Surface Water Chemistry: A Regional Environmental Assessment

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Bivariate and multivariate statistical analyses were used to evaluate the relationships among mapped watershed physical characteristics and surface water chemistry of 122 drainage lake systems in the Northeastern U.S. and 35 drainage stream systems in the Southern Blue Ridge Province. Soils, vegetation, bedrock geology, depth-to-bedrock, wetlands, and land use were mapped on these watersheds at a scale of 1:24,000 with a six acre minimum delineation. The areal extent of these attributes on the watersheds and within close proximity of the subtending surface waters were determined

using GIS ARC/INFO. The proportion of these attributes on the respective drainages were used as regressors in multivariate regression models. Using various model selection techniques, models were developed that describe surface water ANC, sum of base cations, pH, sulfate, DOC, and silica. Watershed attributes explain a considerable amount of variation in the surface water variables. However, in the Northeast, deposition is the greatest source of sulfate and consequently explains most of the variations in sulfate across that region.

Direct Reading X-ray Densitometer

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X-ray densitometry methods were pioneered in France by Polge in the early 1960's. By 1980, there were about 30 laboratories in 18 countries engaged in densitometry work. At Forintek, a computerized X-ray film densitometry system has been in operation since 1971. Recently, a Direct Reading X-ray Densitometer (DRXRD) was developed to make tree-ring measurements more cost efficient. Streamlining sample preparation was the first priority to make X-ray densitometry more efficient. To be cost-effective and to ensure reliability the design incorporated off-the-shelf items wherever

possible. A twin-blade sample preparation saw was built. It is capable of cutting unmounted 5mm diameter increment cores to a uniform 1.5mm thickness. DRXRD offers rapid measurement of ring width and ring density. The detail in which annual rings can be evaluated permits assessment of heterogeneity in wood density within individual annual rings. Such information can be correlated with environmental conditions, silvicultural practices, air pollution, strength properties, tree growth and other variables to a greater degree than gross wood density measurements.

Basis for Using $^{13}\text{C}/^{12}\text{C}$ Ratios in Tree Rings for Retrospective Monitoring of Local/Regional Air Pollution

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Stable-carbon isotope fractionation models provide a guide to how pollutants may influence $^{13}\text{C}/^{12}\text{C}$ ratios ($\delta^{13}\text{C}$) in plants. Generally, if a pollutant reduces the rate of carbon fixation and/or increases stomatal conductance, lower $^{13}\text{C}/^{12}\text{C}$ ratios may be expected, and vice versa. On the basis of reported effects of pollutants on various plants, the following may be expected: for sulfur dioxide, increased fixation if nutritive but decreased otherwise and increased stomatal conductance at high humidity; for carbon dioxide, increased fixation if nutritive and decreased conductance; for ozone, decreased fixation with chlorosis and reduced conductance; for nitrogen dioxide, reduced fixation and uncertain effects on conductance. In

principle, the fixation conductance effects of CO_2 are reinforcing to produce elevated $^{13}\text{C}/^{12}\text{C}$ ratios, and the effects of SO_2 are reinforcing to induce reduced $^{13}\text{C}/^{12}\text{C}$ ratios. Previously reported growth chamber results with SO_2 , however, suggest enzyme injury may inhibit the normal selectivity for ^{12}C over ^{13}C . A field test study to prove the value of tree rings for retrospective monitoring should (1) preferably be at a site which has experienced fumigation primarily from only one of these pollutants, (2) pool tree rings from several radii of each tree cored at the affected site and control site to ensure a representative sample, and (3) analyze the cellulose component of dendrochronologically-dated tree rings.

Grouping Soils Mapped Across a Region into Classes for Sampling for Regional Environmental Assessment

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A primary objective of the Direct/Delayed Response Project is to estimate how many lakes and streams within the Northeast (NE) and the Southern Blue Ridge Province (SBRP) will become acidic due to current or altered levels of acidic deposition, and on what time scales. Because many more soils than were practical to sample were identified during the mapping phase of the soil survey implemented in support of this objective (about 350 named soil components on 145 watersheds in the NE, and about 300 on 35 SBRP watersheds), the soils were grouped into sampling classes of

soils that are thought to be similar with respect to those characteristics that might be more important for predicting the response of lakes and streams to continued acidic deposition. The process of grouping soils was based on the accumulated knowledge and experience of the soil scientists and the insights of the watershed modelers. The result was an acidic deposition hierarchical soil classification system for each region. The 38 NE sampling classes followed soil taxonomy fairly closely; this was not true for the 12 SBRP classes.

Estimates of Tree Crown Areal Histories by Tree Ring Analysis: Use in Throughfall Studies

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Northern red oak crown areas were estimated for two forested sites by a two step procedure using annual growth ring chronologies and published regression equations. The usefulness of crown area estimates in throughfall studies was demonstrated by applying nutrient ion exchange data collected beneath northern red oak crowns in 1984 to 1982, and 1930 crown area estimates. Smaller nutrient ion estimates in 1930 were due to smaller crown area estimates. Application of these techniques

for estimating historical ion exchange chemistry in forest canopies would require modifications to increase accuracy. Competition and stand dynamics need to be considered, and regression equations should be validated. Accurate estimates of past ion exchanges in crowns require knowledge of past trends in atmospheric chemistry. A better understanding of the relationship between throughfall chemistry and chemical and physical variables in canopies is also needed.

Regional Predictions of Surface Water Acidification

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Recognition of acidic deposition as an environmental issue led to the formulation of an important policy question: What is the regional prognosis for acidification of surface waters? The Direct/Delayed Response Project (DDRP) was developed to provide a scientific basis for answering this question. A statistically representative set of 260 lake and stream watersheds was selected and studied in three broad geographic regions covering 14 states. Within the statistical framework, the watershed-specific results are extrapolated to each region and relationships are evaluated between surface water chemistry and watershed characteristics.

To achieve its objectives, the DDRP required a multi-regional terrestrial data base. Soil mapping and soil sampling on each watershed provide information about existing soils,

forest vegetation and land use, bedrock geology, and depth-to-bedrock. Geographic Information System (GIS) and laboratory chemical analyses are used to evaluate which soil or other watershed characteristics determine the long-term response of surface waters to acidic deposition. Procedures of the USDA National Cooperative Soil Survey were incorporated to promote regional consistency and representativeness. A rigorous Quality Assurance and Quality Control program was followed to promote and document product quality. Protocols and procedures used in the broad DDRP soil survey have important implications for developing future programs concerning global climate change and wetland preservation.

*Detailed to the U.S. Environmental Protection Agency, Corvallis, Oregon.

Biochemical Responses of *Pinus sylvestris* and *Picea abies* to Dust Pollution

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Cement dust (CD) can contain a complex of substances not especially toxic for plants, but that have pH higher than 12.7. Dust fallout at a distance of about 1 km from the CD emission centre, where our field experiments were carried out, ranged from 460 to 830 g/m² annually. High Ca and K concentrations in the CD causes alkalinization of the soil (pH 8.1) and precipitation (rain from 7.6 to 9.1; snow, 10.4 to 11.4). CD also causes changes in the cation and anion content of soil and precipitation as well.

Moisture interacting with CD forms crusts on vegetative organs, thus, creating different light, temperature and water regimes in the tissues. This causes metabolic deviations in dusted plants. In dusted needles of *P. sylvestris*, the content of chlorophylls and carotene is decreased and winter maximum of carotene ar-

rises earlier and more rapidly than in controls. In dusted *P. abies* needles, carotene needles are low throughout the year.

Both CD and fuel combustion products from cement plants contain sulphur substances. This is the direct cause of the increase of free SH-groups, SO_4^{2-} and total S in plant tissues. The variations of the ratio of $\text{SO}_4^{2-}/\text{SH}^{-1}$ may provide a basis for interpretation of alterations in S metabolism. The greatest deviations are indicated in mineral composition of plants under CD pollution.

In most cases, visible injuries on the needles were not observed; however, inhibition of radial growth and decrease in thickness of needles was observed in *P. sylvestris*.

A Comparative Study of X-ray Densitometry and Image Analysis for Measuring the Characteristics of Narrow Tree Rings

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A study was conducted to determine the relationship between annual variations in maximum latewood density, ring width and the maximum percent cell wall area present in the latewood of narrow and wide growth rings. The material analyzed represents a tree-ring series across the sapwood-heart wood boundary from *Pinus ponderosa* var. *arizonica* from New Mexico. Variations in measurements obtained by the different analytical procedures within and

between specimen indicate image analysis is the most precise method for narrow growth rings. However, the sample analyzed in this study, which was obtained from a dry site, does not have high sensitivity (0.067) compared to ring width (0.469) or even maximum latewood density (0.124). The maximum latewood density is highly correlated with the maximum percent cell wall area present in the latewood with a $R^2 = 0.78$.

Modifications of SO₂ Injury by Biological Active Substances

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Sulfur dioxide (SO₂) is one of the most widespread air pollutants affecting plants. A plant's response to this gas, however, depends on gas concentration and duration of exposure. Modification of the dose dependence response of pea plants to gas stability modifiers—ascorbic acid, MgCl₂, CaCl₂ and DMSO—were observed and characterized by S-form curves.

The results of these investigations confirmed our assumptions that lipids are one of the possible targets. Presence of liquid crystallized lipids and intensification of lipids peroxide oxi-

dation related directly to increased pollutant concentration. Chemical stability modifiers were observed to reduce formation of liquid crystallized lipids as well as the level of lipid peroxide oxidation. These data indicate that antioxidation effects play a definite role in the protection mechanism provided by ascorbic acid, MgCl₂ and CaCl₂; however, DMSO action is more complex and is evidently related to changes in the membrane matrix. Many things are not yet clear and this problem requires new investigations.

Chemical Analysis of Field-moist vs Air-dried Forest Soil Samples

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The purpose of this study was to quantify the differences, if any, between field-moist and air-dried soil samples, as a function of soil horizon, using standard analytical procedures. Soil samples were collected from six major research sites in the Spruce-Fir Research Cooperative. Samples were split into those maintained at field-moisture content and those air-dried prior to analysis. Fifty-five soil horizons were represented in the study.

A preliminary summary of pH (water) and exchangeable calcium are presented. Within sample variance for soil pH was very small; average standard deviation (wet and dry samples) for five replicates was 0.03 pH units. This suggests that the soils were mixed. Differences between soil samples kept field-moist and those air-dried are apparent, although all 55 horizons have not been analyzed and data has not been fully validated. For this reason, no statistical analyses are presented.

Sulfate Adsorption Characteristics of Soils in the Northeastern U.S.

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US Environmental Protection Agency

Sulfate is the dominant anion in acidic deposition and the principal mobile anion in many surface waters; thus, sulfate retention can be an important process in delaying or preventing acidification of surface waters. As part of an EPA project to predict future surface water acidification, soils were mapped and sampled in 145 lake watersheds in the Northeastern U.S.; water and phosphate extractable sulfate pools and additional sulfate retention capacity (based on nonlinear adsorption isotherms) were measured in ca 1800 soils sampled in these watersheds. Data from individual soils were ana-

lyzed to define relationships between soil and surface water sulfur parameters. Data will be presented summarizing statistical relationships between soil sulfate data (sulfate pools and derived isotherm parameters) and lake sulfate variables (concentration and input-output budget status). Predictions of future changes in soil and surface water sulfate (concentration, time to steady state sulfur budget) will also be presented, based on use of adsorption isotherm and deposition data with a deterministic sulfate adsorption model.

Aggregation of Soil Chemical and Physical Data for Regional Assessment of the Relationship Between Soils and Surface Water Chemistry

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and Oak Ridge National Laboratory

The Direct/Delayed Response Project was initiated by the USEPA to study the relationship between watershed soil properties and surface water chemistry and to make regional predictions about the future surface water chemistry. The data for the project was obtained from 145 lake watersheds in the Northeast U.S. and 39 stream watersheds in the Southern Blue Ridge Province. The soils on these watersheds were mapped and related soil components were grouped into classes for sampling. The soil samples were aggregated to a watershed level

quantity in a manner such the characteristics of each watershed were preserved. The aggregation used differential weighting of the soil classes occurring on a watershed, with the weights based on horizon thickness, soil bulk density, soil hydrologic group, soil depth, position on the landscape, or proximity to surface water. A variety of aggregation models were investigated; the selected method optimized the linear relationship between watershed soil and physical properties and surface water chemistry.

Sampling Design for a Region Based on Soils Mapped

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A primary objective of the Direct/Delayed Response Project (DDRP) is to estimate how many lakes within the Northeast (NE) and the Southern Blue Ridge Province (SBRP) will become acidic due to current or altered levels of acidic deposition, and on what time scales. The objective of soil sampling within DDRP was to determine the mean and variability of soil properties within sampling classes (38 in the NE, 12 in the SBRP) that had been designed to represent all soils found on the DDRP watersheds (145 watersheds in the NE, 35 in the SBRP). When the effects of the terrestrial component of a watershed on a lake or stream are estimated,

it will be assumed that each soil has the properties of the sampling class in which it falls; this will be done regardless of whether that specific soil was sampled. To obtain samples that collectively represented regions and not specific watersheds, sampling sites for each class were randomly selected on watersheds that were themselves randomly selected from those on which the class occurred. Consistency of sampling across regions was maintained by developing uniform protocols, by training crews at regional workshops, and by a rigorous Quality Assurance/Quality Control program.

Correlation and Control of Soil Mapping Across a Region

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Soils and other watershed characteristics were mapped in a few months, across a multi-state region, and by several soil scientists. One uniform legend for the region was controlled by a Regional Coordinator/Correlator (RCC). A preliminary regional soils legend was developed before field mapping began. Mapping quality was controlled through special training, written mapping protocols, state level field review, and field review by the RCC. Mapping protocols specified mapping end products and

responsibilities. Weekly telephone conference calls were used to discuss problems, coordinate work and track progress. The field review process allowed for soil correlation on individual watersheds and on watersheds within a state. Soils and soil map units were correlated during a regional workshop. The mapping design and correlation process provided a quality regional soils database for analyses of the effects of acidic deposition on surface waters in the region.

Dynamic Standardization of Tree-ring Species

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A cumulative sum procedure, commonly used in industrial quality control, has been adapted to aid the fitting of a simplified version of the compound growth function along the lines suggested by Warren (*Tree Ring Bulletin* 40 (1980) 35:44).

The parameters of the function $a \exp(-ct)$ are estimated from the first few ring widths of a series. The fit is projected to the next ring. Consistency with the established trend is analogous to an industrial process being "in control," departure from the established trend, analogous to the process being "out of control." If the cumulative sum indicates an "out of control" situation, the projection is extended to the next few rings to see if the condition persists or if the cumulative sum quickly returns to its "in control" level. The latter suggests that the "out of control" indication is simply a chance event such as must, from time to time, be expected. In this case or when the projection is "in control,"

the parameters of the increment function are re-estimated with the latest point included, and the procedure repeated. If the "out of control" indication persists, it is assumed that a real change in the growth trend has occurred. The fitting of the original function is terminated and a fresh function, of the same general form, fitted from the estimated point of departure. Several goodness-of-fit checks are made on all fitted segments. The same procedure can be applied to any assumed form for the increment function.

The procedure is modular and can be applied interactively with the user overriding "decisions" that he or she judges to be biologically unreasonable. Its objective is to reveal times at which the natural growth trend is affected by endogenous or exogenous disturbances. Also, it may reveal whether the reductions in growth rate experienced in recent times are more rapid than those that occurred in the past.

Biological Markers of Environmental Contamination as Predictors of Human Health and Ecological Effects

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The effect of environmental contamination on human health and ecological integrity is a topic of increasing concern. Unfortunately, a large gap exists in capabilities to either quantify exposure to chemical and physical agents in the environment, or to assess the biological significance of such exposure. Exposure cannot be readily quantified by measuring body burden of contaminants because many deleterious agents do not bioaccumulate, but are rapidly metabolized. Furthermore, the relation between body burden and toxic response is complex and not fully understood. Assessing the significance of exposure to complex mixtures of chemicals, the most realistic environmental scenario, is even more problematic.

Our approach to quantifying exposure and its potential impact is to monitor biological endpoints in feral animals as indicators of adverse effects. The organisms function as inte-

grators of exposure, accounting for abiotic and physiological factors that modulate the dose of toxicant taken up from the environment.

Three elements are critical to our approach: (1) markers selection based on toxicological mechanisms; (2) field studies to establish correlations between environmental contamination and markers; and (3) laboratory confirmation of causal relationships between exposure, biological markers, and adverse effects. Laboratory studies establish dose-dependent relationships between exposure, quantitative changes in a suite of biological markers, and long-term adverse effects.

Although our work has concentrated on aquatic ecosystems, the techniques and rationale are applicable to a wide range of environmental contamination problems.

Site and Stand Characteristics of Southern Appalachian Spruce-Fir

Black Mountains, North Carolina

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Evidence for the decline of southern Appalachian spruce-fir forests as a result of atmospheric deposition of pollutants has recently been reported by many authors. Although it is generally accepted that the growth of southern Appalachian spruce-fir forests has decreased over the past two decades, the connection of this decline to pollution may be circumstantial. Key issues in the debate over the involvement of air pollution center around the expected normal behavior of spruce-fir stands, and their behavior relative to gradients of pollution deposition. Extreme variation in the characteristics of the present stands, ranging from second growth plantations on logged and burned areas to virgin forests, necessitates a detailed assessment of stand characteristics before reasonable expectations of normal behavior can be developed.

A current assessment at three sites indicates that species composition changes dra-

matically with elevation from dominance by red spruce at low elevation to dominance by Fraser fir at higher elevations (>6000 feet). Total stand basal area decreases with increasing elevation and the pattern is consistent with site quality. The percent of dead basal area increases with increasing elevation for both spruce and fir. Red spruce crown vigor has decreased between 1985 and 1987 in the Black Mountains (NC) and the Great Smoky Mountains (TN, NC) but not on the Mt. Rogers National Recreation Area (VA). The decreases in crown vigor are more pronounced at low elevation and in stands heavily dominated by fir. Fir mortality is highly correlated with the occurrence of the balsam woolly adelgid. The current total basal area in even-aged stands is consistent with basal area projections for stands of similar age and site quality.

Response of Seedlings and Mature Trees of the Same Genotype to Ozone

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and

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Growth: Both juvenile seedlings and mature tree ramets of the same genotype were negatively affected by ozone. The magnitude and direction of change may be useful for predicting stand response based on seedling response. Seedling height was more sensitive to ozone than ramet height, with a reduction of 17 percent compared to 11 percent for ramets. Ramet diameter increment was more sensitive to ozone, being reduced by 12 percent compared to 7 percent for seedlings. The relationship between juvenile and mature tree responses was consistent for each parameter measured, i.e., 6 percent greater height reduction and 5 percent less diameter reduction for seedlings vs. mature trees. Half-sib slash pine seedlings were grown for 16 weeks after sowing, and mature grafted trees, for 56 weeks in open-top chambers that were charcoal filtered (CF) or fumigated 5 days per week at 150 ppb ozone. The seed and scions were from the same parent

tree. Seedlings had only one main stem growth flush.

SEM: Needles were taken from the first 1987 and first 1988 flush on a CF and an O₃ treated ramet from each of the 3 clones. The 1987 needles were fully expanded before fumigation began and the 1988 needles expanded under fumigation treatment were 22 cm long. Results to date indicate: 1) Stomatal openings to stomatal chambers of 1988 needles were about 80 percent larger in O₃ treated needles. 2) O₃ treated needles had closed or only partly opened stomata. 3) The O₃ treated needles had a fine net-like wax layer over the guard cells. 4) The CF treated needles had large globular wax plugs or large rod-like wax plugs over the guard cells. 5) 1987 needles expanded under ambient conditions did not lose their large wax plugs even after a year in ozone fumigation.

Effects of Ozone on Water Relations in Bean Leaves

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Elevated concentrations of ozone cause, first of all, changes in cell walls and plasmalemma. Some characteristics of cell walls and plasmalemma can be estimated from relationships between leaf water content and xylem water potential. We have measured relative changes in leaf water content following corresponding changes in xylem water potential of bean leaves in ozone-treated plants. Two fumigation regimes were used: 1) exposure of shoots for 3-4 hours under high (0.6 ppm) ozone concentration, and 2) exposure for 24-48 hours under lower (0.2 ppm) ozone concentration.

After ozonization, the plant shoot was cut near the stem base and let to transpire until its turgor was lost. Then the stem base was closed into a pressure bomb containing water. A leaflet of the first trifoliate leaf was closed into a leaf chamber equipped with a β -gauge for monitoring the leaf water content.

The pressure in the bomb was increased stepwise by 50 kPa until the leaf water content stopped increasing (infiltration was avoided).

Treated leaves absorbed water at significantly lower rates and to a smaller extent than the leaves of control plants. In the case of the first ozonization regime, the increase in water content was the smallest and sometimes only temporary. The absolute water content of ozone treated leaves was also lower. It was found that the limits of the water content corresponding to the turgor region of leaves was smaller in ozone-treated plants. It means that an ozone treated leaf may lose less water before the turgor loss. It was established that the parameter $(1-a)E^*(x_m - x_o)/x_m$ was a constant in our experiments, and did not depend on ozonation. Here x_m is the maximum water content, x_o is the water content before raising xylem water potential, E is the elastic modulus of the leaf, and $a = \Delta WP_\pi / \Delta WP_a$ is the coefficient determining the way the osmotic potential WP_π changes after a change in apoplast water potential WP_a . It was concluded that the amount of osmotically active substances and the stretching capacity of cell walls of bean leaves decreases simultaneously after fumigating the plant.

Response of Loblolly Pine to Acidic Precipitation and Ozone in Alabama

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Concern about damage to forest vegetation due to air pollutants has increased dramatically in the past several decades. Several organizations, including the U.S.D.A. Forest Service and U.S. EPA, have initiated major research programs to assess the impact of air pollutants on forest ecosystems. As a member of the Southern Commercial Forest Research Cooperative (SCFRC), the School of Forestry, Auburn University is part of this assessment. As part of this long-term project (1987-1992), an intensive site has been developed at Auburn, Alabama to study the effects of acidic precipitation and O₃ on growth, biomass production, nutrient status and physiological responses of loblolly pine (*Pinus taeda* L.) growing in the coastal plain of Alabama. Two 6-month-old half-sib families differing in sensitivity to atmospheric deposition, were planted in January, 1988 in modified open-top chambers (15' x 16'). Twelve treatments are replicated twice in a

randomized complete block design. The treatments are a factorial arrangement of 3 levels of acidic precipitation (pH's 5.3, 4.3, 3.3) and 4 O₃ concentrations (carbon-filtered, non-filtered, 1.7 X ambient and 2.5 X ambient). Trees will be grown in the chambers for 3 years, with periodic harvests to remove competitive effects of the trees. During the course of each growing season, intensive measurements will be taken on tree height, diameter, cumulative growth/flush, visible injury, photosynthesis, water relations, nutrient status, biomass production and carbohydrate status. In addition, root biomass production and rhizosphere chemistry will be determined after the 1988 growing season. Results from this study will provide valuable information on the response of loblolly pine to acidic precipitation and O₃, and will provide a better understanding of the manner in which these pollutants might affect tree seedlings and saplings.

Ozone Fumigation of Two Ortets of Eastern White Pine from Acadia National Park, Maine, USA

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A needleblight of eastern white pine (*Pinus strobus*, L.) has been observed in Acadia National Park, Maine, since 1984. Symptoms appear very similar to the previously described semi-mature tissue needle blight (SNB) and include chlorotic and necrotic spots, and chlorotic bands which later advance to pink, orange, and brown necrotic bands with subsequent needle tip necrosis. As with SNB, the cause of this most recent blight remains unknown but both ozone and needle invading fungi are being investigated as etiological agents. Two ramets derived from "SNB symptomatic" ortets in Acadia National Park were exposed to four ozone treatments. Clones C-6, C-13 and wild-type seedlings in Continuously Stirred Tank Reac-

tors were exposed 7 hours a day from May 31 to August 11 to ozone levels at: 1) 15-30 ppb; 2) 40-70 ppb; 3) 40-70 ppb with an early season (June 9) 90 ppb lh spike; and 4) 40-70 ppb with a 90 ppb early season spike and an additional (June 30) 160 ppb lh spike. SNB-like symptoms developed only on clone C-13. Banding and tip necrosis were first noticed in treatments 3 and 4 following the first spike exposure. SNB symptoms became more intense involving additional tissues following the second spike. Exposures to low doses in treatment 2 induced SNB-like symptoms late in the exposure period. Treatment 1 trees remained asymptomatic as did the wild-type and C-6 ramet.

Monitoring of Red Spruce and Balsam Fir Decline in the Northeastern United States: Symptomatology and Mortality Mapping

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A regional multiyear red spruce and balsam fir decline survey, initiated in 1984, is underway in the northeastern United States. This survey encompasses several overall objectives which include assessing and monitoring the amount and distribution of mortality, tree condition and rate of change, stocking and condition of regeneration, and role of historically important damage agents. To address these major objectives, several projects have been designed including a symptomatology project and a mortality mapping project.

The specific objectives of the symptomatology project are to determine the frequency, geographic variability, and progression of crown symptoms, and also to determine which of those symptoms were caused by identifiable damage agents. This project is being conducted in New York, Vermont, New Hampshire,

Massachusetts, and West Virginia. Permanent plots are in place and are visited annually. Various crown symptoms and several biotic and weather related causal agents have been observed.

The specific objectives of the mortality mapping project are to map the locations of red spruce and balsam fir mortality in New York, Vermont, New Hampshire, and western Maine, and to determine the acres of mortality by various cover types and elevational zones. The areas are being mapped from color infrared aerial photographs acquired in 1985 and 1986, and the Maine Geographic Information System is being used to analyze the information and produce the acreage tables and mortality maps. This will provide a baseline to assess the trend of red spruce and balsam fir mortality in the northeastern United States.

Towards Proxy Weather Data: The Association between Tree-Rings and Climate as Revealed by Temporal and Spatial Mapping

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A computerized mapping system was developed at the Canadian Climate Centre for comparing tree-ring data with weather records. It is designed to give quick visual impressions of distributional patterns and comparisons of tree-ring growth and climate (in color) over large geographic areas and long periods of time.

Maximum tree-ring density was compared with August temperatures for six "regions" in central Canada. Both types of data were grouped into three category levels: "high," "medium" and

low." The period of analysis was from 1800 to 1984, but the weather data extend back only to 1903. Maximum ring density is a good measure of August temperature. Of the 347 instances where both tree-ring and weather data are available, only 18 (5.2%) gave "opposite" results (one parameter "high" and the other "low").

The system can be expanded geographically and temporally and other tree-ring and weather variables can be used.

Appendix

Symposium Program

SESSION I DENDROECOLOGY—TREE RINGS AND ENVIRONMENT

Papers

1. The US-USSR Cooperative Project—A Brief History, *Juri Martin*
2. U.S. Forests and Atmospheric Deposition, *Jack Winjum*
3. Logfren Comparative Analysis of the Standardization Methods of Tree-Ring Chronologies, *Stepan Shiyatov*
4. Dendrochronology and Environmental Factors, *Edward Cook*
5. Three-Ring Reconstruction of Mean June-July Temperature Using Siberian Larch Tree-Ring Series, *Donald Graybill*
6. Simulative Model on Tree-Ring Tracheidogram on the Base of Climatic Variables, *Evgeny Vaganov*
7. Dendrochronology and Spatial Analyses, *Gregory Reams*
8. Dendrochronology and Forest Ecology, *Linda Brubaker*
9. Selecting Analysis Procedures for Tree-Ring Data when Estimating the Effect of Exogenous Disturbances, *Michael Arbaugh*

Jeff Brandt, *Moderator*

Workshop

Detecting Effects of Cumulative Exogenous Disturbances in Tree-Ring Series
Harold C. Fritts, William G. Warren, Michael J. Arbaugh, *Moderators*

Working Sessions

Jeff Brandt, *Moderator*
Beverly Law, *Program Coordinator*

SESSION II MECHANISMS AND ALTERNATIVE HYPOTHESES

Papers

1. Air Pollution, Plants and Mechanisms: A Historical Perspective, *Ellis Cowling*
2. Diagnostic Physiology and Biochemistry Studies on Loblolly Pine (*Pinus taeda* L.), *Thomas Sasek*
3. Impacts of SO₂ Fumigation on the Ultra-Structural and Photosynthesis of Pine Needles. Part I. Mesophyll Cells, *Irina M. Kravkina*
4. Impacts of SO₂ Fumigation on the Ultra-Structural and Photosynthesis of Pine Needles. Part II. Resin Duct Cells, *Andrey E. Vasilyev*
5. Impacts of SO₂ Fumigation on the Ultra-Structural and Photosynthesis of Pine Needles. Part III. Transition Zone, *Richard Crang*
6. Ozone Concentration in Leaf Intracellulars is Close to Zero, *Agu Laisk*
7. Forest Decline and the Winter Injury Hypothesis, *Ruth Alscher*
8. Mechanisms by which Regional Air Pollutants Affect Forest Soils and Rhizospheres, *Daniel Richter and Michele Schoenberger*
9. Mechanisms of Genetic Control of Air Pollution Tolerances in Forest Trees, *David Karnosky*

10. Air Pollution Impact on Structure and State of Northern European Forest Ecosystems, *Vladislav Alexeyev*
11. Simulating Tree Level Processes, *Cheryl Gay*
12. Tree to Ecosystem Extrapolation, *Jack Waide*

Ann Bartuska, *Moderator*

Workshops

Physiological and Morphological Comparisons Between Seedlings and Trees

Robert Teskey, *Moderator*

Linkages: Trees vs. Ecosystem

James N. Woodman, *Moderator*

SESSION III BIOINDICATION AND PROTECTED AREA MONITORING

Papers

1. Monitoring the Environment in the 21st Century, *Stanley I. Auerbach*
2. The Great Smoky Mountains Biosphere Reserve, *John Peine*
3. (Soviet) Lichens as Bioindicators of Metal Deposition, *Oleg Blum*
4. Biomarkers of Environmental Contamination, *John McCarthy*
5. Comparative Estimates of the Effects of Ozone, Sulphur Dioxide and Nitrogen Dioxide on Plant Productivity, *Sergei M. Semjenov*
6. Bioindication of Air Pollution Effects, *Leonard Weinstein*
7. Element Accumulation in Lichens, Mosses and Soils Connected with Mud Volcanos Activity, *Juri Martin*
8. A National Program for Environmental Monitoring and Assessment, *Jay Messer*
9. Managing for Biological Diversity, *Christine Schonewald-Cox*
10. Monitoring for Exotic Species, *Peter White*
11. A National Vegetation Survey, *Lewis Ohman*
12. Monitoring and Detecting Climate Change, *Frank Quinlan*
13. Climate Change and Forest Resources, *Robin Graham*
14. Direct Effects of CO₂ on Trees, *Richard Norby*
15. Modeling Effects of Climate Change, *William Emanuel*

David Shriner, *Moderator*

Workshop

Global Climate Change

Robert M. Cushman, *Moderator*

Planning Session

Future Research Cooperation

David Shriner, Reginald Noble, Juri Martin, *Moderators*

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Corvallis, Oregon
September 13 - 14, 1988

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To commemorate the 10th year of cooperation between the US-USSR in the field of environmental protection, a symposium was organized, the major objectives of which were to acquaint US-USSR scientists with project accomplishments; to promote understanding of the nature of environmental problems that relate to air pollution effect on vegetation on a more global scale; to share research priorities, interests, and methodologies; and to plan future research cooperation.

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